Grassland Breeding Bird Response to Landscape, Climate, and Spring Burning in the Tallgrass Prairies of Kansas

By

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ABSTRACT

Given the drastic loss of prairie habitat and consequent decline in grassland bird populations, identifying the factors that influence habitat selection by grassland birds has become a critical tool for effective conservation management. This study investigated habitat occupancy by grassland birds in the Kansas Flint Hills tallgrass prairie during the 2000-2010 breeding season. Boosted regression tree models were used to relate species presence to explanatory variables representing landscape, climate, and prescribed spring burning for fifteen grassland bird species. The impact of spring burning on the diversity and structure of grassland bird communities was also examined, using a selection of diversity indices and paired distance matrices correlating similarity and geographic distance. The effect of burning on community structure was further illuminated through nonmetric multidimensional scaling ordination. All occupancy, diversity, and similarity analysis was based on data obtained from the U.S. Breeding Bird Survey (BBS), and evaluated at BBS stop level.

ACKNOWLEDGEMENTS

This project began with a visit to the Flint Hills National Wildlife Refuge in Hartford, Kansas with my advisor extraordinaire, Dr. Stephen Egbert. There, we met with Mike Estey, a biologist with the USFWS Habitat and Population Evaluation Team (HAPET), who showed us a map of spring burning in the Flint Hills. I will forever be grateful to Dr. Egbert for his friendship, his thoughtful guidance, his gentle nudges, and for being my most enthusiastic cheerleader. Thanks also to my committee members: Dr. Terry Slocum, Professor Emeritus, for his painstaking (though sometimes painful) editing of my work and for cheerfully 'Skyping' in from Alaska; and Dr. Bill Johnson, for graciously stepping into the breach after the sudden passing of Dr. Bill Woods. And I am, of course, deeply indebted to Rhett Mohler, then a PhD candidate at a rival (and so unnamed) university in Kansas, for creating and kindly sharing his burn maps with me. Rock Chalk!

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CHAPTER 1: INTRODUCTION

Abstract

Globally, temperate grasslands are among the most imperiled, yet least protected ecosystems. In North America, conversion of native tallgrass prairies has exceeded 99% in some areas, and those grasslands that remain are often negatively impacted by fragmentation, encroachment by woody vegetation, and intensive range management strategies. The drastic loss and alteration of this habitat is reflected by a corresponding decline in grassland bird populations in North America that is greater than any other avian ecological or behavioral group. In the tallgrass prairie region of Kansas, annual spring burning of grasslands is used to suppress woody vegetation and non-native species, and improve forage for cattle. By reducing litter depth and removing standing dead vegetation, fire impacts not only the aboveground patch structure of prairie vegetation, but depending on the fire return interval and other factors, can alter plant community composition as well. Since habitat structure plays a critical role in determining habitat use by birds, the frequency, pattern and extent of disturbance by burning potentially impacts the occurrence, diversity, and composition of grassland bird communities.

I. Background

Native grasslands have been called "the least conserved, most altered landscape on earth" (The Nature Conservancy, TNC, 2014). Because global habitat conversion exceeds habitat protection by 10 to 1 for temperate grasslands, savannas, and shrublands, these regions are considered 'Critically Endangered', a designation analogous to the International Union for Conservation of Nature (IUCN) Red List for Species (Hoekstra, et al., 2005). Prior to European

settlement of prairie states, native grasslands represented the largest vegetative province in North America, roughly 17% of the continent, and covered approximately 162 x 10^6 ha, (Knopf, 1988; Samson & Knopf, 1994). The area of native tallgrass prairie has since declined by an estimated 82.0-99.9%, a loss greater than any other biome including the old growth forests of the Pacific Northwest (Samson & Knopf, 1994). Yet despite this loss, only 0.5% of the original tallgrass prairie extent is protected in some way (Steinauer & Collins, 1996). Where expansive tracts remain, such as in the Flint Hills and Osage Plains of Kansas and Oklahoma, it was often because shallow rocky soils and rough terrain made the areas too difficult to plow (Steinauer & Collins, 1996). Although at least 82% of pre-European settlement tallgrass prairie acreage in Kansas was lost, what remains represents 80% of all tallgrass prairie remaining in North America, more than all other prairie states combined (Samson, et al., 1998).

The majority of tallgrass prairie acreage in North America was lost to agriculture, primarily cereal grains (Samson & Knopf, 1994), but native prairies were also converted to agricultural grasslands (hayfields and pasture, often planted to exotic grasses), which are now the dominant grassland habitat throughout much of the tallgrass region (Vickery, et al., 2000). Agricultural mechanization and intensive management, including increased use of agrochemicals, heavy grazing, frequent haying, and either annual burning or fire suppression, are all practices contributing to ongoing grassland degradation that reduces habitat suitability for some bird species and can decrease avian species diversity (Knopf, 1994; Vickery, et al., 2000; Askins, et al., 2007). Where not lost outright to agriculture or development, native grasslands often remain in small, fragmented parcels (Askins, et al., 2007). Encroachment of woody vegetation through fire suppression, expansion of riparian forests, and introduction of forested shelterbelts throughout the Central Plains have also effectively fragmented remaining grasslands

(Samson & Knopf, 1994). In addition, the vertical structure introduced by woody vegetation, uncommon in grasslands prior to European settlement, provides travel corridors and shelter for mammalian predators as well as nest and perch sites for both avian predators and brood parasites, and potentially reduces nest success for grassland birds (Knopf, 1994; Rich, et al., 2004).

Given the profound loss, fragmentation, and degradation of grassland habitat, it should come as no surprise that over the last few decades grassland dependent birds have suffered "steeper, more consistent, and more geographically widespread declines than any other behavioral or ecological guild of North America species, including neotropical migrants" (Knopf, 1994: 251; Peterjohn & Sauer, 1999). Declining populations of grassland and shrubland birds in North America have been described as a "prominent wildlife conservation crisis of the 21st century" (Brennan & Kuvlesky, 2005:1). Although natural variability in distribution make trends for individual species difficult to estimate, continental trends since the mid-1960s support an overall decline in grassland bird populations (Knopf, 1994; Sauer, et al., 2013), prompting groups such as the U.S. Fish and Wildlife Service (USFWS), Partners in Flight (PIF), the National Audubon Society (NAS) and the North American Bird Conservation Initiative (NABCI) to list many grassland birds as species of concern or priority species (USFWS, 2008; Rosenberg, et al., 2014). In fact, nearly 40% of species included on the PIF Continental Watch List, breed in the prairie biome (Rich, et al., 2004). Because most grassland breeding birds are short distance migrants, wintering in the southern U.S. and northern Mexico (Rich, et al., 2004), the population decline is most likely related to processes occurring in North America (Knopf, 1994).

As a guild, grassland birds have been identified as those species that rely entirely or in part on grassland habitats for breeding, nesting, feeding, migration, and/or wintering (Vickery, et

al., 1999). Of the 435 bird species found in the U.S., 330 have been documented as breeding in the Great Plains (Samson & Knopf, 1994). Grassland birds can be roughly grouped as *obligate* or *facultative* species. Vickery, et al. (1999) defined obligates as those species entirely reliant on grasslands for all or part of their life cycle. Without suitable grassland habitat they would likely drastically decline or become extinct. In contrast, facultative species are defined as those species that use grasslands regularly, but not exclusively, and are capable of exploiting a wider range of habitat types than obligate species. In the absence of suitable grasslands, facultative species might decrease in numbers, but would be unlikely to disappear entirely. Throughout North America, Mexico, and the Caribbean, there are only 59 obligate grassland species and 97 facultative grassland species, compared to more than 180 obligate forest species (Vickery, et al., 1999). The drastic loss and alteration of native grasslands threaten the persistence and conservation of all grassland dependent birds, making identification of critical habitat and the selection of appropriate management strategies increasingly important. Conservation efforts of all types often focus on preserving or enhancing biodiversity, so effective natural resource management depends in part on identifying and quantifying the biogeographical and environmental factors, including disturbance, that influence species distribution and diversity (Dornelas, et al., 2011).

II. Landscape, Climate, and Disturbance

Vegetation structure and composition are well known as drivers of local bird abundance (MacArthur & MacArthur, 1961; MacArthur, et al., 1962; Wiens, 1973, 1974b; Rotenberry & Wiens, 1980; Cody, 1981; Zimmerman, 1992, 1997; Patterson & Best, 1996). Whereas species geographic range is more closely aligned with climate, it is local habitat characteristics that

influence selection of territory (Wiens, 1973, 1974a; Cumming, et al., 2014). Differences in vegetation structure and composition provide the spatial heterogeneity that influence avian community diversity (Roth, 1976; Anderson, 2006). Structure may be the most critical aspect of habitat selection (e.g., MacArthur & MacArthur, 1961; Wiens, 1974b; Cody, 1981; George, et al, 1992), but the importance of structure over composition is not always clear (Winter, et al., 2005). For example, Müller, et al. (2010) found that for forest birds, structure appears more important for predicting bird diversity; however, composition appears more predictive for at least one shrub species (Wilsey, et al., 2012). For grassland birds, both structure and composition likely play a role in species distribution (Wiens, 1974b; Rotenberry, 1985; Patterson & Best, 1996). Determining the influence of structure is especially complicated in grasslands as vegetation can change markedly among years at the same site because of random effects relating to weather and grazing (Vinton & Collins, 1997; Winter, et al., 2005), resulting in interannual variation in bird-landscape associations (Riffell & Gutzwiller, 2009) that are likely scale-dependent (Bakker, et al., 2002; Vinton & Collins, 1997)

Habitat area and edge effects are also well known to impact abundance and diversity of grassland birds, but habitat area and edge sensitivity can vary widely depending on species, region, and range management (Herkert, 1994b; Vickery, et al., 1994, 1999; Helzer & Jelinski, 1999; Winter & Faaborg, 1999; Coppedge, et al., 2001; Davis, 2004; Renfrew, et al., 2005; Winter, et al., 2006; Askins, et al., 2007; Ribic, et al., 2009). Samson (1980) found that patch size and isolation were correlated to species richness for birds inhabiting prairie relicts in Illinois, but perimeter-to-area ratio of available habitat may be the stronger predictor of individual species occurrence and overall species richness (Helzer & Jelinski, 1999). The diversity of cover types in the surrounding landscape may also have an impact on avian diversity that can be equal

to or greater than absolute patch size (Roth, 1976; Ribic & Sample, 2001, Bakker, et al., 2002). For some area-sensitive grassland birds, structural features like roads, ponds, fences and woody vegetation can reduce the perceived size of patches (Bakker, et al., 2002; Patten, et al., 2006; Winter, et al., 2000; Coppedge, et al., 2008).

Climate variability, especially periodic drought, along with frequent disturbances by fire and grazing are among factors that shaped and continue to sustain the extent, structure, and function of grasslands in the Great Plains (Anderson, 1990, 2006; Collins & Gibson, 1990; Knopf & Samson, 1997; Knapp & Seastedt, 1998); however, any increase in the irregularity of annual precipitation, resulting in fewer but more extreme precipitation events and more frequent, severe and longer periods of drought, is likely to magnify existing impacts on grasslands from agriculture, grazing, and burning (Knapp, et al., 2002; IPCC, 2014, Shafer, et al., 2014). In Kansas, Knapp, et al. (2002) found that increased rainfall variability, independent from changes in total annual precipitation, reduced above ground growth and dominance of C4 photosynthetic pathway (warm-season) grasses. An overall decrease in growing season precipitation coupled with warming temperatures could exacerbate water deficits and reduce grassland productivity, as well as floristic and functional diversity (Crane, et al., 2011).

Elevated levels of atmospheric carbon dioxide (CO_2) could alter carbon source-sink dynamics in tallgrass prairies, with the magnitude and direction of the effect variable dependent on soil moisture, soil nitrogen (N) availability, soil type, and landscape position (Seastedt, et al., 1998, Owensby, et al., 1999; Knapp et al., 2002; Craine, et al., 2011; Fay, et al., 2012; Polley, et al., 2013). Although C4 perennial grass communities remained relatively stable under conditions of elevated atmospheric CO_2, Owensby et al. (1999) found that C3 photosynthetic pathway (cool-season) grasses declined while C3 forbs increased. Elevated atmospheric CO_2 may also

alter grasslands through an increase in the abundance of woody species, both through enhanced growth of trees and shrubs, which then shade out grasses, and because of changes in prescribed fire regimes that are anticipated in response to increased temperatures and more frequent and prolonged drought (Polley, et al., 2013). Finally, elevated CO_2 and N in concert with warming temperatures could alter plant phenology by advancing the timing of green-up and flowering, delaying flowering in grasses and accelerating it in forbs (Cleland, et al., 2006).

While most grassland birds are adapted to the natural climate variability of the Great Plains, changes in climate may alter avian distribution, abundance, richness, and community composition, as well as result in early arrival at breeding grounds and changes in timing of breeding and clutch size (Butler, 2003; Cotton, 2003; Torti & Dunn, 2005; LaSorte & Thompson, III, 2007; Visser, et al., 2009; Skagen & Yackel Adams, 2012; Cumming, et al., 2014; Gutiérrez Illán, et al., 2014). For example, Butler (2003) found that short-distance migrants arrived at breeding grounds earlier than long-distance migrants, possibly because they relied on meteorological rather than photoperiodic cues to signal migration. Prediction of future distributions is complicated by species-specific traits such as site fidelity and competition (Stralberg & Bayne, 2013), but in general, a shift to higher latitudes is projected for North American species (Hitch & Leberg, 2007; LaSorte & Thompson, III, 2007) and to higher elevations for tropical species (LaSorte & Jetz, 2010). Considering the geographic shift in range distribution and reduction in habitat extent projected for grassland zones, birds of the plains may be more vulnerable to a changing climate than montane species (Peterson, 2003), generalist species, or those capable of long distance dispersal (Skagen & Yackel Adams, 2014).

Increases in temperature and variation in precipitation may also affect bird populations directly through heat stress and water restriction (Wiens, 1974a). Some studies have found that

moisture was more of a determinant than temperature (Zimmerman, 1992; Albright, et al., 2010a; Gutiérrez Illán, et al., 2014; Skagen & Yackel Adams, 2014), but others found that temperature was more influential (Cumming, et al., 2014) or that the impact of temperature and/or precipitation varied among species (George, et al., 1992; Fleishman, et al., 2014). Albright et al. (2010b) found that heat waves and drought in combination were more predictive of changes in abundance than either measure alone. They also found that sensitivity to drought varied depending on life history traits, with declines in abundance more likely in the West and for ground-nesting birds.

The frequency, intensity, and timing of disturbance are also critical to avian biodiversity in grasslands (Wiens, 1974b) and play a key role in the distribution and abundance of grasslands birds (Zimmerman, 1993, 1997; Knopf, 1994; Reinking, 2005; Askins, et al., 2007). Disturbance can increase biodiversity by freeing up resources and by at least temporarily changing community dynamics, assuming species adapted to different environmental needs are able to exploit the altered conditions (Dornelas, et al., 2011). Where disturbance results in an increase in habitat heterogeneity, as reflected in the number of locally available habitats and/or their structural complexity, resources and niche opportunities should expand, facilitating the coexistence of species and leading to more diverse communities (MacArthur & MacArthur, 1961; Tews, et al., 2004). Conversely, when habitat loss or disturbance reduces habitat heterogeneity and niche availability contracts, species that are more limited in the resources they can exploit (ecological specialists) are likely to be less abundant because they are more limited in an ecological sense (LaSorte, 2006).

In tallgrass prairies, fire is likely the most influential disturbance (Anderson, 1990; Collins & Wallace, 1990; Knopf, 1994; Collins & Steinauer 1998); however, prescribed fires

differ in seasonality, frequency, and scale from those ignited by lightening or set by American Indians prior to European settlement (Anderson, 1990; Engle & Bidwell, 2001). Where widespread burning occurs frequently, the local habitat stays more open and less structurally complex, with a reduction in litter depth, standing dead vegetation, and woody vegetation, but more bare ground (Knopf & Samson, 1997). In contrast, where fire is suppressed, grasslands are degraded by the encroachment and eventual dominance of woody vegetation (Collins, 1992; Briggs, et al., 2002). Woody vegetation may begin to dominate some unburned grasslands after ten years (Abrams & Hulbert, 1987; Collins, 1992; Glenn, et al., 1992; Collins & Steinauer, 1998; Briggs, et al., 2005), with a closed tree canopy forming in 40 years (Briggs, et al., 2002). In fragmented grasslands, however, even burning every three years may not be enough to maintain open grasslands (Davison & Kindscher, 1999). Fire suppression over decades may cause irreversible changes in grassland bird community composition (Grant, et al., 2010); in contrast, the homogenous landscape that results from extensive annual burning may irreparably threaten the viability of some grassland bird populations, even in grasslands of large extent (With, et al., 2008).

Burning acts in the short term as an abrupt change in the above-ground canopy structure; post-burn succession leads to taller vegetation, increases in standing dead vegetation, accumulation of litter, and eventual encroachment by trees and shrubs (Brawn, et al, 2001; Briggs, et al., 2005). The loss of plant biomass due to prescribed fire results in at least temporary displacement of certain avian species, especially those that prefer a more heterogeneous habitat (Brawn, et al., 2001). Avian species richness may vary depending on time since burning, being lowest in the first post-burn growing season but returning to pre-burn status within two to three years (Zimmerman, 1992; Robel, et al., 1998; Swengel & Swengel, 2001; Coppedge, et al., 2008;

Grant, et al., 2010; Roberts, et al., 2012). The assemblage shift is likely transitory because birds occupy adjacent unburned habitat rather than disappear completely (Grant, et al., 2010). Burning can impact reproductive success by removing the vegetative structure that some species depend on for nesting or attracting a mate (Zimmerman, 1971, Robel, et al., 1998), but may also affect bird survival by impacting the availability of food. For example, fire combusts some seeds, but removes litter that may hide other seeds, and although insect mortality results from fire, remaining insects may be easier to find (Best, 1979). Although it is unclear how edge- and area-sensitive species are impacted, burning might effectively fragment grassland habitat by creating distinct patches and edges (Collins & Wallace, 1990). Conversely, where fire is suppressed, edges associated with encroaching woody vegetation may also have a negative impact, even when woody cover is not extensive (Winter, et al., 2000; Coppedge, et al., 2001, 2004; Chapman, et al., 2004; Patten, et al., 2006). Whether the changes in habitat structure occur through burning or post-burn succession, patch size may still be more predictive of avian community composition and abundance (Herkert, 1994a).

III. Research Overview

The primary objective for this research was to develop exploratory models investigating the relative influence of landscape, climate, and disturbance by fire on the occurrence of certain grassland bird species in the Kansas Flint Hills, from 2000-2010. For individual species, the intent was to discover whether habitat occupancy was related to the variables of interest, and to determine whether the relative importance of the variables differed depending on a species' preference for open grassland habitat versus shrubby or wooded areas. A secondary objective was to examine the grassland bird community response to the occurrence of burning in a single

year and the cumulative number of burns over the study period. For single years, assemblage structure in terms of diversity and similarity at sites where burning occurred was compared to sites that were unburned. In addition, average diversity and community similarity over the study period were compared at sites where burning was frequent versus sites where it was rare.

Overview of Approach and Methods

The effect of prescribed fire on grassland birds has been evaluated in numerous studies in grasslands (e.g. Zimmerman, 1997; Robel, et al., 1998; Madden, et al., 1999; Walk & Warner, 2000; Swengel & Swengel, 2001; Reinking, 2005; Fuhlendorf, et al., 2006; Churchwell, et al., 2008; Hovick, et al., 2012); however, most previous research investigated the impact of burning in concert with grazing, involved experimental studies rather than exploratory models, and focused on a limited number of specific bird species rather than examining similarity in assemblage. This project is unique in the modeling method used, the length of the study period and breadth of the study area, and the focus on the cumulative effect of burning on assemblage structure. In addition, species occurrence is determined based on publicly available, long-term count data as is commonly used by conservation agencies for monitoring bird populations, rather than demographic data obtained from a limited number of treatment/control plots.

In this study, individual boosted regression tree (BRT) models were used to analyze the occurrence of fifteen breeding bird species in the Kansas Flint Hills region relative to variables reflecting climate, landscape composition, and the pattern of prescribed spring burning over an 11-year period. Boosted regression is an ensemble 'machine-learning' (ML) method that, like a simple decision tree model, uses an algorithm to subdivide feature space into regions with shared characteristics or similar responses to the predictor (Breiman, et al., 1984; Elith, et al., 2006,

2008; De'ath & Fabricus, 2000; De'ath, 2002, 2007). Unlike conventional regression models, ML methods explore dominant relationships among the data without an *a priori* assumption that a specific, parsimonious data model is most appropriate or even known (Breiman, et al., 1984; Elith, et al., 2006). Although not yet considered mainstream, BRT models are gaining acceptance in species distribution modeling, especially for ornithological studies. BRT models are nonparametric, an attribute particularly important in species distribution modeling as the distribution of both abundance and presence-absence data will likely be non-normal (Elith, et al., 2008). In addition to modeling the occurrence of selected individual species, this study examined the impact of disturbance by prescribed spring burning on grassland bird community structure, both in response to the occurrence of fire in a single year and as a function of the frequency of burning over the study period.

Several studies have used comparable approaches to modeling grassland bird species distribution, including investigating the impact of disturbance on bird populations. For instance, Patten, et al. (2006) used a simple regression tree analysis to investigate how edge effects and range management (undisturbed, grazing, and a single year of burning) impacted rates of brood parasitism in tallgrass prairie habitat of northeastern Oklahoma. O'Connor, et al., (1999) also used a simple classification and regression tree analysis to examine the influence of climate, agriculture, and landscape pattern on the continental distribution of 17 grassland bird species, but, they did not consider the impact of any disturbance. Wilsey, et al. (2012) used an ensemble decision tree model to map potential habitat for a single shrub species in Texas. Their modeling method, a variation of the Random Forests classification algorithm (Breiman, 2001) rather than boosted regression, was similar to the one used for this study, but their study focused on the utility of LiDAR data to derive landcover variables and did not investigate the impact of

disturbance on occurrence. With, et al. (2008) examined the same general region with the same burn frequency data used for this study, but theirs was a two-year demographic analysis of three grassland birds rather than an occupancy model.

Study area and data

A. Study Area

The Flint Hills region extends in a north-south band across eastern Kansas and into northern Oklahoma and represents the largest contiguous unplowed tallgrass prairie (1.6 million ha) remaining in North America (Knapp & Seastedt, 1998; Askins, et al., 2007). The region has a humid continental climate, with hot summers, cool to cold winters, moderately strong surface winds, highly variable annual precipitation and frequent drought; average annual precipitation is 825mm, most falling in the spring and summer (Samson & Knopf, 1994; Abrams & Hulbert, 1987). The area is characterized by rolling hills, relatively steep valleys, and limestone outcroppings; upland areas have shallow, rocky soils that are drier, less productive, and more variable in soil moisture relative to the deeper soils of the floodplains (Knapp, et al., 2002; Briggs, et al., 2005; Frey, et al., 2008). Topography and geology made the area generally unsuitable for agriculture but not for ranching (Abrams & Hulbert, 1987, Knapp & Seastedt, 1998). Croplands exist, but are restricted to the lowland floodplains. Trees and shrubs occur along fencerows, shelterbelts, and in gallery forests along watercourses, as well as where burning has been suppressed. More than 600 plant species have been documented in the Flint Hills (Knapp & Seastedt 1998); dominant warm season grasses of the uplands are big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), with blue grama (*Bouteloua gracilis*), sideoats

grama (*B. curtipendula*), and buffalograss (*B. dactyloides*) on more xeric sites (Abrams & Hulbert, 1987; Freeman, 1998).

The study area (Fig. 1) encompassed 16 counties that overlap the majority of the Kansas portion of the Flint Hills physiographic region: Butler, Chase, Chautauqua, *Coffey*, Cowley, Elk, Geary, Greenwood, Lyon, Marshall, *Marion*, Morris, Pottawatomie, Riley, Wabaunsee, and *Woodson* (counties listed in italics are adjacent to, but not considered among the 13 core counties of the Kansas Flint Hills region). The study area boundary matches one used by Mohler (2011), who created the burned area maps on which this project is based. Approximately 90% of the grasslands are held in large, privately owned parcels (Towne & Owensby, 1984; Fitzgerald, et al., 2000). The grassland area within each county ranges from 171,128 ha (87% of total land area) in Chase County to 71, 259 ha (67% of total) in Geary County; Marshall County had the lowest percentage (33%) of grassland area (77,514 ha) (Mohler & Goodin, 2012). In general, counties on the periphery of the Flint Hills have less total grassland area, often represented as fragmented grasslands interspersed with cropland as well as smaller grasslands enrolled in the Conservation Reserve Program (CRP) (Mohler, 2011). The CRP is a federally funded private-lands conservation program wherein landowners, in exchange for yearly rental payments, voluntarily agree to take environmentally sensitive lands out of agricultural production and seed them with approved plant species mixes, thereby re-establishing land cover that will reduce soil erosion, improve water quality, and increase and improve wildlife habitat.

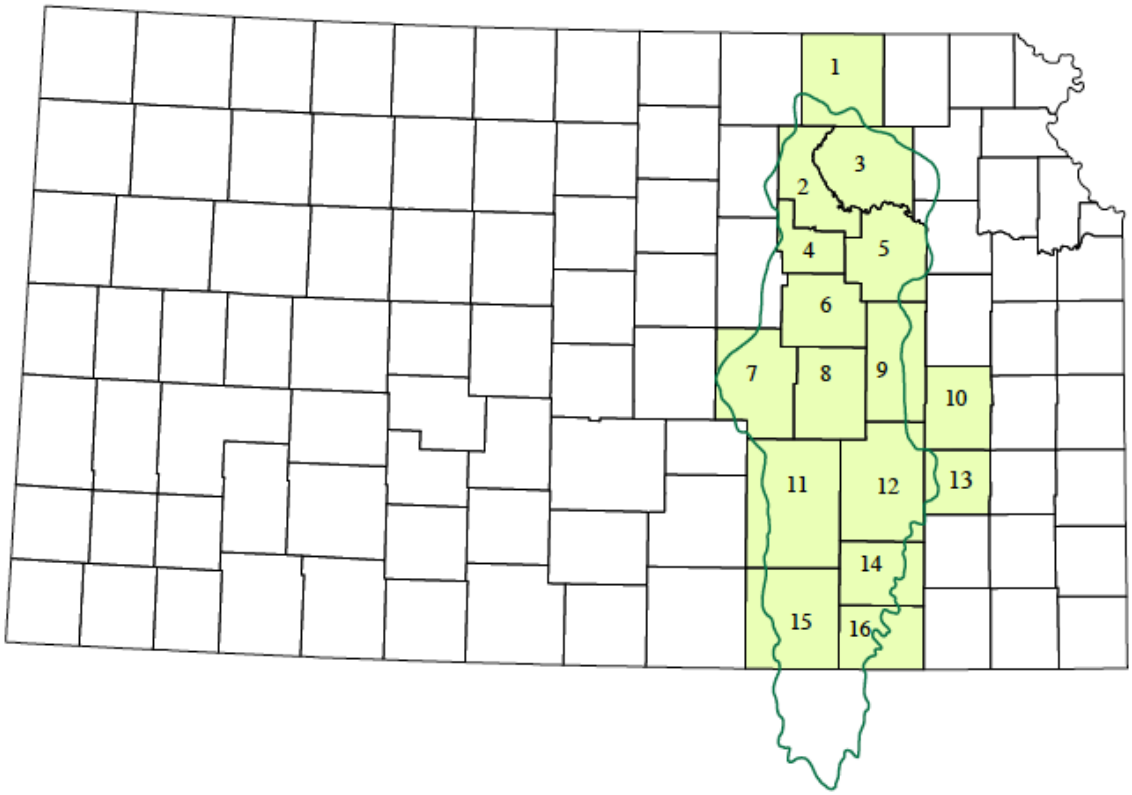


FIGURE 1. Kansas map showing study area counties shaded in green, with the Flint Hills Level III Ecoregion boundary (EPA, 2013) outlined in darker green. County names: 1) Marshall, 2) Riley, 3) Pottawatomie, 4) Geary, 5. Wabaunsee, 6) Morris, 7) Marion, 8) Chase, 9) Lyon, 10) Coffey, 11) Butler, 12) Greenwood, 13) Woodson, 14) Elk, 15) Cowley, and 16) Chautauqua.

B. Species Data

Species presence was determined based on count data taken from the North American Breeding Bird Survey (BBS), a large-scale, long-term international monitoring program administered jointly by the U.S. Geological Survey (USGS) and the Canadian Wildlife Service to track the status and trends of North American breeding bird populations (Bystrak, 1981, Pardieck, et al., 2017). The BBS was initiated in 1966 in response to concerns over pesticide effects on birds; by 2010 there were 5267 routes recorded for the US, Canada, and Mexico, with more than 3100 routes surveyed annually (Bystrak, 1981; Sauer, et al., 2013). BBS routes follow

secondary and tertiary roads; starting point and direction were randomly selected when the route was initiated. Individual routes are 39.4 km (24.5 miles) long and consist of 50 stops, spaced at 800m (0.5 miles) intervals. Surveys begin 30 minutes before local sunrise. At each sequential stop, an observer conducts a 3-minute point count, recording all birds seen or heard within a 400m (0.25 mile) radius and making note of weather condition, traffic, or other factors that might influence total counts. Surveys recorded under unacceptable conditions or on dates or times outside of acceptable range are flagged. Routes are surveyed annually, usually in June although starting dates in late May in southern states and early July in northern states and Canada are acceptable (Robbins, et al., 1986). Although ten BBS routes overlap the study area, only the seven routes that lie completely within the study area counties were examined (Fig. 2).

The BBS was designed as a roadside survey, so routes may not be random with respect to available habitat or be located where birds truly representative of the area are likely to be encountered. For example, roads in western mountainous regions often follow waterways, so riparian species may be oversampled, but in the plains states, roads more often cross than parallel riparian forests, so woodland species could be undersampled (Droege, 1990). BBS route locations throughout the United States were found to poorly represent higher elevations and drier regions (Lawler & Connor, 2004), as well as permanent wetlands and open water (Niemth, et al., 2007; Veech, et al., 2012). Across the continental United States, Lawler & O'Connor (2004) found that deciduous forests were overrepresented, although in Ohio, Bart et al. (1995) found less forest cover within 140 meters of roads compared to that 140-280m away. Veech et al., (2012) evaluated more than 3200 BBS routes across the conterminous United States to determine the proportion of 15 cover types in surrounding landscapes. While overall error for most classes was fairly low (typically +/− 4%), misrepresentation occurred for more common cover types,

including pasture, grasslands, shrubland, and forest. Routes also may not reflect the larger landscape because more rapid and intensive development (e.g. residential and commercial development, forest clearing, etc.) happens adjacent to roads rather than farther away. In Ohio and Maryland, Keller and Scallan (1999) examined habitat within 200m of BBS routes compared to that 200-1600m distant and found statistically significant differences between the two areas, mostly for cover types associated with human activities.

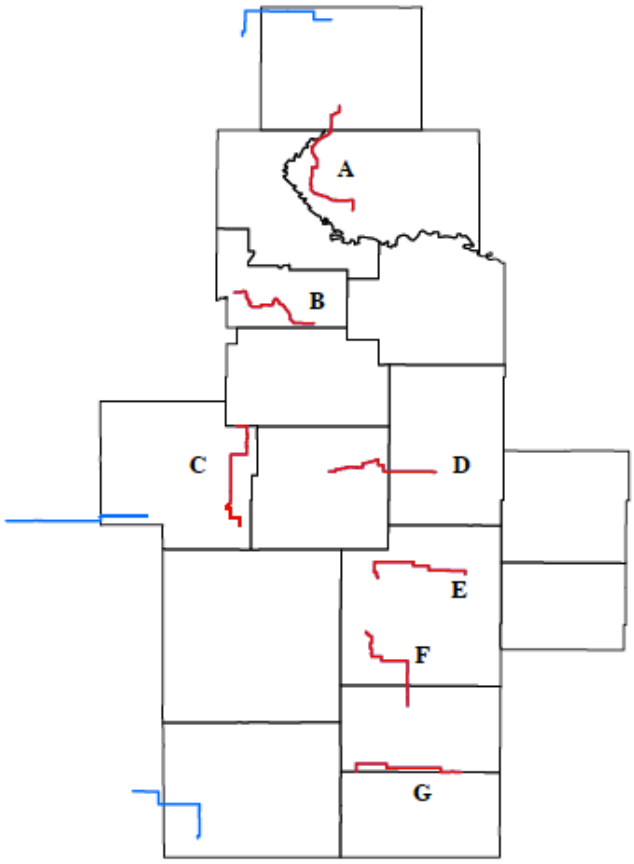


FIGURE 2: Breeding Bird Survey (BBS) routes that overlap the study area are shown in red and blue. Only the 7 routes shown in red were examined for this study. BBS routes names are: A. Olsburg, B. Wreford, C. Lincolnville, D. Ellinor, E. Lapland, F. Reece, and G. Longton.

The impact on species population estimates can depend on the degree of disparity between the route and the larger region it is intended to represent, and on whether this misrepresentation changes over time. Multiple studies have examined BBS routes in comparison with surrounding landscapes, most often focusing on the effect of roadside bias on bird counts (e.g. Bart, et al., 1995; Griffith, et al., 2010; McCarthy, et al., 2012); however, few have specifically addressed the issue of proportional habitat representation and its impact on population estimates. For example, Wellicome et al. (2014) looked at BBS roadside bias in Canadian grasslands, comparing both landcover percentages and bird populations, and found that offroad areas had greater grassland area and almost twice the number of bird species, including grassland species of conservation concern. Niemuth et al. (2007) studied route/habitat representation for 12 cover types within 400m of 52 BBS routes in the Prairie Pothole regions of North Dakota and South Dakota and found that existing BBS routes were representative of surrounding areas for most cover categories except upland grass patches and wetlands, leading to potentially flawed population estimates for grassland species and waterbirds.

Thesis Contents

In Chapter 2, the focal species selected for modeling are identified and the habitat preferences and response to disturbance expected for each species are summarized. Functional trait differences between the focal species, particularly those that might impact the accuracy of population estimates, are discussed. The machine learning method used to model the selected grassland species is explained in detail, including the approach used to optimize the model parameters for each species model. The explanatory variables used for each model are described, as is the model simplification process used to remove uninformative predictors. An

evaluation of model fit and predictive performance is presented for each species individually and in comparison to other species with similar and different habitat requirements. The relative importance of predictors retained in each species model is analyzed. Relative importance plots are presented, as are partial dependence plots showing the fitted functions for the five most influential variables.

Chapter 3 explores the impact of annual burning on avian diversity and community composition. Using the same set of annual BBS survey data used in Chapter 2, stops were grouped according to the presence of burning within the stop buffer (*Burn, NoBurn*) in an individual year. Differences in diversity between burn groups was evaluated using common diversity indices, including richness, and abundance. The magnitude of difference in mean index values was used to gauge the strength of any differences found. Rank abundance curves, kernel density estimation diagrams, and box plots were used to visually compare mean abundance and richness between groups. Community composition within and between burn groups was investigated using dissimilarity matrices. The statistical significance of any difference in community structure within and between burn groups was assessed using nonparametric analysis of similarity (ANOSIM, Clarke, 1993) and nonparametric multivariate analysis of variance (NPMANOVA, Anderson, 2001). The relationship between community similarity and geographic distance was evaluated using the ordination method of nonmetric multidimensional scaling (NMDS, Clarke, 1993). Chapter 4 summarizes the findings detailed in chapters 2 and 3, highlighting their implications and outlining areas of potential future research.

CHAPTER 2: SPECIES OCCUPANCY MODELING

Abstract

Species occupancy models were built for fifteen bird species known to occur within the Flint Hills tallgrass prairie region of Kansas. Focal species varied in their habitat requirements, with some preferring open grasslands, with others more likely to be found in grasslands with taller grasses, heavier litter, and/or woody vegetation. Boosted regression tree (BRT) modeling was used to relate species presence to a suite of explanatory variables representing landscape, climate, and disturbance by prescribed spring burning. BRT models were constructed for individual species and additionally for species grouped according to habitat specificity (grassland obligate, grassland facultative, and shrub-woodland). Individual and groups models were evaluated based on fit, predictive performance, and relative variable influence.

I. Background

Breeding Bird Survey

For this study, species occupancy was modeled at the Breeding Bird Survey (BBS) stop rather than route level for both individual and group models. Although not without flaws, the BBS is a key source of information for population change for more than 400 bird species in North America; for most species it is the only source of population and distribution data (Sauer, et al., 2003). BBS count data are considered an index of abundance rather than absolute abundance since not all species can be sampled equally or completely (Bystrak, 1981; Thogmartin, et al., 2006). Several factors can contribute to variation in BBS data separate from changes in bird populations, particularly in relation to roadside sampling (Bart, et al., 1995;

Hutto, et al., 1995; Rotenberry & Knick, 1995; Griffith, et al., 2010) and observer effects (Link & Sauer, 1998; O'Connor, et al., 2000). Observer quality varies between individuals, over time, and in different habitats, and includes differences in counting ability that relate to first time observer effects, changes in skill over time, or differences in hearing ability (Faanes & Bystrak, 1981; Emlen & DeLong, 1992; Sauer, et al., 1994; Kendall, et al., 1996). Variability in sampling efficiency can also result from local species richness (Scott & Ramsey, 1981) or abundance (Bart & Schoultz, 1984), or because familiarity with the route introduces expectation as to what species should be present (O'Connor, et al., 2000).

Imperfect detection has been recognized by the BBS as an issue since its inception (O'Connor, et al., 2000; Sauer, et al., 2013), and defining the extent of potential bias and determining viable solutions to overcome it is a priority according to a recent BBS Strategic Plan (USGS, 2007). Detection probability can vary by: 1) avian density (Bart & Schoultz, 1984); 2) observer (Faanes & Bystrak, 1981; Sauer, et al., 1994; Kendall, et al., 1996); 3) habitat structure (Anderson, et al., 1981; Richards, 1981; Bibby & Buckland, 1987); and 4) survey conditions, such as time of day (Robbins, 1981b; Skirven, 1981), season (Best, 1981; Skirven, 1981), weather (Robbins, 1981a), and ambient noise (Richards, 1981; McCallum, 2005). Several methods have been proposed to estimate and account for unequal species detection probability in point counts (e.g., Thompson, 2002; McCallum, 2005; Johnson, 2008; Buckland, et al., 2011), but were not part of BBS methodology for routes surveyed during the study period. Because the population data used for this study were not collected using these methods, the occupancy models presented here did not directly address detection heterogeneity. Detection probability between species is unlikely to be equal, but occupancy models were created for each focal species individually. Because of the relatively open terrain across the study area, stops were

presumed to be equivalent enough to each other in terms of visible and auditory obstructions that detection probability for an individual species was not appreciably different between stops.

Occupancy and abundance estimates are based on the assumption of random sampling and equal detection of all species (Boulinier, et al., 1998; Gotelli & Colwell, 2011), so not accounting for detection probability in species occupancy modeling has the potential to bias some model results (MacKenzie, et al., 2002, 2003; McCallum, 2005; Johnson, 2008; Buckland, et al., 2011). Because BBS methods don't "guarantee either a census or a known fixed area of sampling" (Link & Sauer, 1998:261), absolute abundance can't be directly observed or independently validated and therefore the magnitude of bias introduced by imperfect detection can't be measured with certainty. Welsh, et al. (2013) found that ignoring detection probability in occupancy models introduced bias and high variance, but no more so than when detection probability was included. In their BRT models, Fleishman, et al., (2014) found that including detection probability did not change the relative influence of predictors or increase the explained deviance. Although detection heterogeneity was not included as a model variable, an attempt was made to reduce other known biases by excluding data from annual surveys conducted on invalid dates, times or under adverse conditions, as well as data from annual routes surveyed by a first-time observer (on that particular route). Data from the single annual survey not censused at all stops were also omitted.

Boosted Regression Model

By sequentially fitting a collection of single trees, BRT modeling addresses the problem of overfitting and instability known to impair simple decision tree methods (O'Connor & Wagner, 2004; Elith, et al., 2006; Hastie, et al., 2009; James, et al., 2013). Each new tree

focuses on the poorly fitted observations from previous iterations; trees fitted early on reveal the more general and clearly defined patterns in the data while trees fitted later expose more detailed features (Elith, et al., 2008). Stochasticity is introduced by training each sequential tree using a preselected bootstrap sample of the training data (the *bag fraction,* ***bf***). Using random subsets of data improves accuracy, increases computation speed, and helps to reduce overfitting (Freidman, 2002). To optimize BRT models, BRT modeling requires that users preset other metaparameters as well (De'ath, 2007; Elith, et al., 2008; Hastie, et al., 2009). In addition to the bag fraction, modelers must preset a "learning rate" (***lr***), which controls how much each tree contributes to the expanding model; the tree complexity (***tc***), which defines the level of interaction allowed between predictors; and the number of boosting iterations (i.e., trees, ***nt***) (Elith, et al., 2008). The goal of this model calibration, or "tuning", is to balance fit with performance. For example, a slower ***lr*** typically decreases test error but must be balanced by increasing the number of trees built, which in turn increases computation time (De'ath, 2007; Elith, et al., 2008; Hastie, et al., 2009). For models with a relatively small number of observations (e.g. 250), a ***tc*** setting of 2-3 and an ***lr*** slow enough to generate at least 1000 trees is recommended (Elith, et al., 2008).

Metaparameter calibration means that models can be customized for specific projects and data sets; despite this flexibility, BRT models are still not commonly used in ecological studies (Elith, et al., 2008; Olden, et al, 2008). Although considered by some to be less interpretable (Elith, et al., 2008), BRT models are ideal for analyzing complex ecological data and are particularly well suited for data exploration and prediction (O'Connor & Wagner, 2004; De'ath & Fabricius, 2000; De'ath, 2002, 2007; Elith, et al., 2006; Olden, et al., 2008). BRT models are nonparametric, an attribute particularly important in species distribution modeling as the

distribution of both abundance and presence-absence data will likely be non-normal (Elith, et al., 2008). As with other algorithm-based, machine learning (ML) methods, data sets that include mixed variables, nonstandard data structures, outliers, and missing data are easily accommodated, with little data preprocessing required (Breiman, et al., 1984; De'ath, 2007; Elith, et al., 2008; Olden, et al., 2008; Hastie, et al., 2009). Variable interactions are modeled automatically, with the user determining whether main effects only or higher-level interactions will be allowed. Because feature selection is fundamental to the tree-building process, irrelevant features are rarely selected and redundant or correlated variables are largely ignored (Elith, et al., 2008; Hastie, et al., 2009); however, including correlated or redundant variables, especially where data sets are small, can create overly complex models that may hinder interpretability and degrade model accuracy and/or predictive performance (Elith, et al., 2008; Hastie, et al., 2009).

Several studies have shown that algorithm-based, machine learning methods outperformed traditional statistical methods when modeling ecological data (Elith, et al., 2006; Leathwick, et al., 2006; Moisen, et al., 2006; De'ath, 2007; Oppel, et al., 2012), especially when sample sizes are small (Wisz, et al, 2008). Algorithm-based methods have been used in ecological studies to examine the distribution of soft coral on the Great Barrier Reef (De'ath & Fabricius, 2000), the variation in demersal fish species richness (Leathwick, et al., 2006), the difference in distribution and response to disturbance between diadromous and non-diadromous fish (Leathwick, et al., 2008), and the determinants of reproductive success in clownfish (Buston & Elith, 2011). Other studies have compared machine learning to other modeling methods: to examine the impact of prevalence, latitude and aggregation on butterfly species distributions (Marmion, et al., 2009), to predict the future distribution of coyotes (McCue, et al., 2014), and to explore the influence of landscape scale and species autecology on the relative importance of

climate/non-climate predictors for kangaroos (Harris, et al., 2014). Plant species have also been modeled: comparing different functional groups of pasture plants (Zhang, et al., 2005); examining the error associated with extrapolating local abundance data to a regional extent for plants on the Central Plains (Young, et al., 2012); and predicting tree species presence and basal area (Moisen, et al., 2006).

ML methods, including simple decision trees, have been applied in ornithological studies as well: for predicting the continental distribution of forest bird species richness (O'Connor & Wagner, 2004); for examining the abundance and temporal incidence of grassland birds across the conterminous U.S. (O'Connor, et. al., 1999); for targeting areas for forest bird conservation (Jones-Farrand, et al., 2011); for modeling the occurrence of urban birds (Meffert, et al., 2012); for examining the effect of in-site habitat variables on forest birds (Yen, et al., 2011); and to study forest bird response to microhabitat variables in clear cuts of different age and size (McDermott, et al., 2011). ML models have been used as well to compare forest and shrub bird abundance across two time periods in response to projected climate change (Cumming, et al., 2014; Fleishman, et al., 2014) and to model presence and abundance related to spatial variation in climate predictors (Gutiérrez Illán, et al., 2014). In addition to modeling species distribution, BRTs have been used to examine nest site selection of hooded cranes (Jiao, et al., 2014), to determine habitat associations during seabird nesting season (Raphael, et al, 2014), and to explore how model characteristics vary with life history of ducks (Barker, et al., 2014). ML methods have also been used to model the distribution and species richness of forest and shrub birds based on landscape variables derived from unclassified Thematic Mapper reflectance values (Shirley, et al., 2013) and from LiDAR returns (Goetz, et al., 2007; Wilsey et al., 2012).

Although algorithm-based ML methods are more robust to spatial autocorrelation (SAC) in response variables than statistical methods (Elith, et al., 2008; Harris, et al., 2014), the reliability of biogeographical analyses can be compromised when sample sites are close geographically (Lichstein, et al., 2002; Betts, et al., 2006; Algar, et al., 2009). A well-constructed BRT model with sufficient and relevant explanatory variables will show little SAC; however, the presence of SAC in model residuals can indicate that key environmental parameters are missing or that geographic influences predominate (Elith & Leathwick, 2009). For this study, each part of the modeling process (training, validation, and testing) used a subset of BBS stops selected randomly without replacement from the total set of stops available. Since stops within each subset could be adjacent, close geographically, or represent the same stop in different years, stop locations were used as an explanatory variable to account for broad scale spatial relationships, and model results were also evaluated for residual spatial autocorrelation (RAC) using Moran's I correlogram (Lichstein, et al., 2002).

Focal Species

The focal species modeled included five obligate grassland species: Dickcissel (*Spiza Americana*), Eastern Meadowlark (*Sturnella magna*), Grasshopper Sparrow (*Ammodramus savannarum*), Upland Sandpiper (*Bartramia longicauda*), and Western Meadowlark (*Sturnella neglecta*); five facultative grassland species: Brown-headed Cowbird (*Molothrus ater*), Common Nighthawk (*Chordeiles minor*), Mourning Dove (*Zenaida macroura*), Northern Bobwhite (*Colinus virginianus*); and Red-winged Blackbird (*Agelaius phoeniceus*)**;** and five shrub/open woodland species: Bell's Vireo (*Vireo bellii*), Carolina Wren (*Thryothorus ludovicianus*), Field Sparrow (*Spizella pusilla*), Red-headed Woodpecker (*Melanerpes erythrocephalus*), and Yellow-

billed Cuckoo (*Coccyzus* americanus). The focal species, along with their common and scientific names, American Ornithological Union (AOU) 4-letter Alpha Code (Pyle & DeSante, 2014), and other information are listed in Table 1. Focal species were selected in part based on their status as priority or focal species and/or birds of conservation concern according to the US Fish and Wildlife Service (USFWS) Migratory Bird Program (USFWS, 2008), the Partners in Flight (PIF) North American Landbird Conservation Plan (Rich, et al., 2004), the North American Bird Conservation Initiative (NABCI) State of the Birds 2014 Report and Watch List (NABCI, 2014; Rosenberg, et al., 2014), the National Audubon Society (NAS) WatchList 2007 (Butcher, et al., 2007), and the USFWS Flint Hills Legacy Conservation Candidate Priority Bird Species List (Mike Estey, USFWS, pers. comm.). Relative abundance and distribution across the study area and over the study period was also considered. The focal group was composed of seven taxonomic orders (Caprimulgiformes, Charadiiformes, Columbiformes, Cuculiformes, Galliformes, Passeriformes, and Piciformes); all are represented by a single species except Passeriformes, which had nine species in five families (Cardinale, Emberizidae (with two species each), Icteridae (four species), Troglodytidae, and Vironidae).

In addition to habitat specificity, focal species vary in nesting substrate, foraging strategy, breeding season diet, and migratory pattern. Among the species modeled, birds that nest on the ground were the most common, but several nest in shrubs, trees or cavities, such as the Bell's Vireo or Carolina Wren. Two species, the Common Nighthawk and the Brown-headed Cowbird, construct no nests at all, the former laying eggs directly on bare ground or even flat gravel rooftops, and the latter laying its eggs in the nests of other bird species (brood parasitism). For the Mourning Dove, nest substrate is variable, with birds nesting on the ground, in trees, on buildings, or using the old nests of their own or other species. Excepting a single granivore

(Mourning Dove), the focal group was split evenly between omnivores and insectivores based on predominant breeding season diet. Most feed on the ground, using either a foraging or gleaning strategy in equal measure, but several use the shrub/low-canopy as the foraging substrate. Common Nighthawks feed almost exclusively in the air, whereas Red-headed Woodpeckers feed both in the air and as bark gleaners.

TABLE 1: Focal species.

Common Name	Scientific Name	AOU code*	Abundance	Presence	# Surveys
Bell's Vireo	*Vireo bellii*	BEVI	169	149	53
Brown-headed Cowbird	*Molothrus ater*	BHCO	2702	1404	**62**
Carolina Wren	*Thryothorus ludovicianus*	CARW	222	204	44
Common Nighthawk	*Chordeiles minor*	CONI	398	308	54
Dickcissel	*Spiza Americana*	DICK	**5945**	**2362**	**62**
Eastern Meadowlark	*Sturnella magna*	EAME	2983	1527	**62**
Field Sparrow	*Spizella pusilla*	FISP	390	316	50
Grasshopper Sparrow	*Ammodramus savannarum*	GRSP	1183	752	58
Mourning Dove	*Zenaida macroura*	MODO	2679	1357	**62**
Northern Bobwhite	*Colinus virginianus*	NOBO	2022	1356	**62**
Red-headed Woodpecker	*Melanerpes erythrocephalus*	RHWO	**137**	**124**	50
Red-winged Blackbird	*Agelaius phoeniceus*	RWBL	2112	967	**62**
Upland Sandpiper	*Bartramia longicauda*	UPSA	964	657	59
Western Meadowlark	*Sturnella neglecta*	WEME	391	178	**26**
Yellow-billed Cuckoo	*Coccyzus americanus*	YBCU	897	777	**62**

*American Ornithological Union four-letter Alpha Code, AOU, 2016
Numbers listed in **bold** indicate high/low values for each category

The focal group also varied in functional traits and behavior that potentially influence detection probability and therefore estimates of abundance and occurrence (Diehl, 1981; Mayfield, 1981; Wilson & Bart, 1985). For instance, not only do Common Nighthawk adults, young, and eggs have cryptic coloring, but this was also the only crepuscular species modeled. Crepuscular and nocturnal species, as well as raptors, water birds, marsh birds, shorebirds, and boreal and arctic species are difficult to accurately count by standardized census methods like those used by the BBS (Robbins, et al., 1986; Sauer, et al., 2013). The Common Nighthawk was

included because of its significance as a facultative grassland bird and because it was listed on the NABCI 2014 State of the Birds Report as a Common Bird in Steep Decline (NABCI, 2014). Behaviors that make a bird more noticeable can also impact detection. For example, prominent territorial display, defense or vocalizations, such as are demonstrated by the Dickcissel, Carolina Wren, Eastern Meadowlark, and Red-winged Blackbird (Johnsgard, 1979; De Graaf, et al., 1991; Tekiela, 2001), could impact detection by making individuals more conspicuous. Birds that routinely perch on fence posts, wires, shrub or tree tops like the Dickcissel, Upland Sandpiper, and Western Meadowlark (Johnsgard, 1979; Busby & Zimmerman, 2001; Tekiela, 2001) are likely more obvious than the Yellow-billed Cuckoo, whose behavior is more secretive (Busby & Zimmerman, 2001). Similarly, birds with loud or distinctive calls, such as the Dickcissel, Common Nighthawk, Northern Bobwhite, Red-winged Blackbird, and Yellow-billed Cuckoo (Johnsgard, 1979; Busby & Zimmerman, 2001; Tekiela, 2001) may draw attention more than those with a less conspicuous call, like the Grasshopper Sparrow (Busby & Zimmerman, 2001). With some species, vocalizations can vary over time or under certain conditions; for instance, Field Sparrows sing less once nesting has begun (Johnsgard, 1979) and anecdotal evidence suggests that the Yellow-billed Cuckoo earned its colloquial name, the “rain crow” or “storm crow”, based on its apparent habit of calling more frequently in advance of summer thunderstorms (Poole, 2005).

Species-Landscape Relationships

Habitat occupancy preferences of the modeled species ranged from species that favor bare ground or very low vegetation to those that favor shrubby vegetation or open woodland. Tolerance for habitat area and edge also varies. In general, obligate grassland species prefer

more open grasslands, but differ in their tolerance for plant litter, standing dead vegetation, and presence of trees or shrubs. The Dickcissel is associated with grasslands with moderate to tall grasses, a high percentage (>50%) of forbs, and a well-developed litter layer (Johnsgard, 1979; Frawley & Best, 1991; Busby & Zimmerman, 2001; Fuhlendorf & Engle, 2001; Poole, 2005; Askins, et al., 2007). Shrubs and small trees are used for territorial displays, but are not required for patch suitability (Busby & Zimmerman, 2001); however, proximity to dense shrubby or wooded areas may reduce habitat value, in part because of higher nest parasitism (Helzer & Jelinski, 1999; Winter, et al. 2000**;** Tekiela, 2001; Patten, et al., 2006). In Kansas, Dickcissel also use CRP grasslands, hayfields, fallow fields, croplands planted to cover crops like alfalfa, old fields in early succession, and ecologically similar roadside habitats (Johnsgard, 1979; Zimmerman, 1993; Dechant, et al., 1999c; Busby & Zimmerman, 2001; Poole, 2005; Rahmig, et al., 2008). Dickcissel is an area sensitive species that has shown greater density, abundance, and reproductive success in larger (>10 ha) patches (Herkert, 1991, 1994a, 1994b; Swengel, 1996, Winter & Faaborg, 1999); however, probability of occurrence may be negatively impacted by a high perimeter-area ratio (Helzer & Jelinski, 1999).

The Eastern Meadowlark is more abundant in prairies with intermediate height grasses and moderate litter (Zimmerman, 1971; Herkert, et al., 1993; Zimmerman, 1993; Patterson & Best, 1996). Like Dickcissel, Eastern Meadowlarks may also benefit from CRP grasslands (Riffell, et al., 2008, 2010), especially since population declines for both species have been correlated with reductions in pasture and hay acreage in some areas (Herkert, et al., 1996). Eastern Meadowlark will use open croplands of small grains (Johnsgard, 1979), but an increasing percentage of cropland negatively impacts nesting habitat, as does old-field succession from open grassland to woodland (Riffell, et al, 2008, 2010). Larger habitat patches

have been associated with greater relative abundance (Herkert, 1994a, 1994b), but smaller patches may also be of benefit (With, et al., 2008; Walk, et al., 2010). Where their ranges overlap, Eastern Meadowlarks are found in more mesic areas with taller grass and denser forb cover than Western Meadowlarks. In general, Western Meadowlarks are found in more arid native or cultivated grasslands with shorter grass, sparser forb cover, and more vertical patchiness (Dechant, et al., 1999d; Busby & Zimmerman, 2001; Johnson & Igl, 2001; Poole, 2005). Western Meadowlarks are uncommon in croplands (Poole, 2005), but may use the small grassy areas at the corners of center-pivot irrigation fields for nesting (Busby & Zimmerman, 2001). Evidence regarding area-sensitivity is mixed, in part because Western Meadowlark abundance and occurrence varies regionally and annually (Johnson & Igl, 2001).

The Grasshopper Sparrow has experienced widespread population decline in North America (at least 69% across the U.S. since the last 1960s) (Herkert, 1994b), owing in part to changes in grassland management on wintering and breeding ranges (Busby & Zimmerman, 2001). In the Midwest, Grassland Sparrows are positively associated with moderately open grasslands with short to mid-height, clumped vegetation and patchy bare ground (Zimmerman, 1971; Wiens, 1973; Patterson & Best, 1996; Dechant, et al., 1998; Busby & Zimmerman, 2001, Poole, 2005), and negatively associated with areas of greater vertical structure and more visual obstruction (Zimmerman, 1971; Patterson & Best, 1996). Grasshopper Sparrows also inhabit grazed tallgrass, mixed grass, CRP grasslands, and patches of annual weeds (Dechant, et al., 1998; Walk & Warner, 2000; Busby & Zimmerman, 2001; Rahmig, et al., 2008). Scattered trees are acceptable, but areas with dense shrubs are avoided (Johnsgard, 1979). Because Grasshopper Sparrows use exposed bare ground for foraging (Poole, 2005), abundance is generally higher in areas with low to intermediate litter (Swengel & Swengel, 2001); however, nest survival has

been associated with increasing grass and litter cover (Frey, et al., 2008). Grasshopper Sparrow is an area-sensitive species, more likely to occupy larger habitat patches with a smaller perimeter-area ratio (Samson, 1980; Herkert, 1994a, 1994b; Helzer & Jelinski, 1999; Vickery, et al., 2004). The Grasshopper Sparrow shows distinct year-to-year variation in density and is often locally distributed even in areas with similar habitat (Johnsgard, 1979).

The Upland Sandpiper, considered the "signature species for the true prairie community" (Busby & Zimmerman, 2001: 156), is of conservation concern in at least 24 states and provinces (Sauer, et al., 2013). Seventy percent of the breeding population is concentrated in the Great Plains region (Vickery, et al., 2010). In general, Upland Sandpipers are associated with moderate density, short to medium-height grasslands with moderate to high litter, little bare ground, and minimal shrub cover over a large area (Sample, 1989; Herkert, et al., 1993; Dechant, et al., 1999a; Vickery, et al., 2010). Upland Sandpipers are highly area-sensitive (Vickery, et al., 1994; Johnson & Igl, 2001), requiring habitat patches at least 30 ha in size (Dechant, et al., 1999a). Abundance, density, and probability of occurrence have been positively correlated with habitat patch area (Herkert, 1994a, 1994b; Helzer & Jelinski, 1999; Dechant, et al., 1999a) and inversely correlated with perimeter-area ratio (Helzer & Jelinski, 1999). In the Flint Hills, Upland Sandpipers preferentially select hilltops, important for mating activities like display and defense, and favor edge habitats, where heterogeneity is highest (Sandercock, et al., 2015).

Facultative species are by definition more liberal in their habitat requirements than obligates species. The Brown-headed Cowbird was originally restricted to short grass prairies (Poole, 2005), but has become widely dispersed as European settlement cleared forests for agricultural, suburban, and urban use, thus exposing new species to parasitism (Poole, 2005). In Kansas, Brown-headed Cowbirds parasitize at least 50 species including the Dickcissel, Field

Sparrow, Grasshopper Sparrow, Eastern Meadowlark, and Red-winged Blackbird in prairie habitats, as well as the Brown Thrasher (*Toxostoma* rufum), Field Sparrow, Lark Sparrow (*Chondestes grammacus*), and Bell's Vireo in shrubby, wooded areas (Johnston, 1964; Zimmerman, 1993; Busby & Zimmerman, 2001). Although a single egg is laid in each host nest (Johnsgard, 1979), Brown-headed Cowbird females may lay 40 eggs a season (Poole, 2005). Because host species with open nests are less available in prairie habitats, parasitized nests can contain eggs from multiple cowbird females, and heavily parasitized species such as Dickcissel and Bell's Vireo may raise only cowbird chicks (Busby & Zimmerman, 2001). During the breeding season, Brown-headed Cowbirds are most often associated with woodland-grassland edge habitats, as well as brushy thickets and areas where small, scattered trees are interspersed with grasslands, rather than with either extensive woods or extensive grasslands (Johnsgard, 1979; Johnson & Temple, 1990; Poole, 2005).

The Common Nighthawk requires open habitats for nesting and feeding, using native grasslands, dry land agricultural sites, and urban areas (Busby & Zimmerman, 2001). Significant decline in Common Nighthawk numbers over the last few decades could be related to loss of habitat, an increased use of pesticides that leads to a reduction in insect prey, and a switch to new roofing materials that replace gravel on urban buildings (Busby & Zimmerman, 2001; Sauer, et al., 2003; Poole, 2005). Range management that results in grassland conversion to shrubland reduces habitat suitability and abundance (Pidgeon, et al., 2001, 2007). Common Nighthawks are generally single-brooded (Johnsgard, 1979; Tekiela, 2001), but may lay an additional clutch in sites burned annually in the spring (Zimmerman, 1993). Common Nighthawks are active mostly at dusk and after sunset, but in the daytime can also be spotted sleeping on fence posts

(Tekiela, 2001) or during their obvious courtship and pair-bonding flights (Busby & Zimmerman, 2001).

The Mourning Dove is one of the most widespread and abundant birds in North America (Poole, 2005). Vickery, et al. (1999) defined this species as a facultative grassland bird, but it could be also considered a habitat generalist (Poole, 2005). Mourning Doves can be found in open grasslands, croplands, edge habitat between woods and prairie, and in urban and suburban landscapes, avoiding only extensive forests and wetlands (Johnsgard, 1979; Poole, 2005). The Red-winged Blackbird is another very abundant bird species in North America (Busby & Zimmerman, 2001). Although often associated with marshland (Johnsgard, 1979; Zimmerman, 1993), Red-winged Blackbirds also use a wide variety of other upland prairie and agricultural habitats, including pastures, hayfields, grain fields, fallow fields, stream drainages, roadside ditches and weedy areas, urban parks, and suburban areas (Zimmerman, 1993; Busby & Zimmerman, 2001; Poole, 2005). In general, areas with nearby trees and abundant edge habitat are preferred (Poole, 2005).

The Northern Bobwhite inhabits the edge habitat offered by a mix of woody vegetation, cropland and grassland (Johnsgard, 1979; Busby & Zimmerman, 2001; Tekiela, 2001). Herbaceous vegetation must be short enough and sparse enough for birds to walk through, with open areas of nearly bare ground for nesting (Johnsgard, 1979). Cover type diversity provides grassy nesting sites, access to grain crops or a similar food source, brushy cover, and a place appropriate for dusting; access to a nearby water source further improves habitat suitability (Johnsgard, 1979). Where agricultural management practices have expanded field sizes, removed hedgerows, and increased pesticide use, the value of agricultural land as habitat for Northern Bobwhites is lessoned through a reduction in habitat heterogeneity and elimination or

suppression of food sources (Poole, 2005). Abundance between years is highly variable, which may reflect differences in overwintering survival rather than alteration of habitat (Zimmerman, 1993; Busby & Zimmerman, 2001).

The shrub-woodland species modeled in this study depend on habitats with woody vegetation that range from relatively open areas with scattered shrubs and small trees to isolated trees or open woodland. The Bell's Vireo inhabits dense shrubby thickets in dry uplands; larger tracts of riparian scrub along drainages; low brushy patches characteristic of early old field succession; patchy habitat along fencerows, roadsides, forest openings and, in the Flint Hills, dogwood clumps often associated with rock outcrops, seeps, and springs (Zimmerman, 1993; Fitzgerald, et al., 2000; Busby & Zimmerman, 2001). It is rarely found in extensively cultivated areas, pure grassland regions, or forest interiors (Poole, 2005). For Bell's Vireo, surface water and larger patch area seem to be important determinants of habitat use (Poole, 2005).

The Field Sparrow is another species that inhabits areas characteristic of early to mid old-field succession, with moderate to dense shrubs and brush and scattered small trees (Busby & Zimmerman, 2001). In prairie regions, it also uses attenuated riparian forest edges, stream drainages with small trees and patchy shrubs, brushy ravines, and similar areas that offer both low grassy areas and scattered woody vegetation (Johnsgard, 1979; Zimmerman, 1993). The Field Sparrow has shown area-sensitivity, having greater relative abundance in larger habitat patches (Herkert, 1994b). Unlike the Field Sparrow, which does not breed close to human habitation (Poole, 2005), the Carolina Wren may be present in cultivated areas with brush piles and in suburban parks and gardens (Tekiela, 2001). It is often found near homes, inhabiting older urban neighborhoods with habitats ecologically similar to riparian deciduous forests (Busby & Zimmerman, 2001; Poole, 2005).

The Yellow-billed Cuckoo is flexible in its nesting habitat requirements, using closed canopy forests, forest edges, moderately dense thickets in riparian areas and near marshes, second growth woodlands, brushy orchards, small stands of understory trees, abandoned farmlands, and even isolated trees in grasslands (Johnsgard, 1979; Busby & Zimmerman, 2001); however, very dense woodlands and urban areas are generally avoided (Johnsgard, 1979). In Kansas, occurrence declines westward coincident with a decrease in woody vegetation cover (Busby & Zimmerman, 2001). Breeding habitat for the Red-headed Woodpecker tends more toward open woodland, with larger, wide-spaced trees and a grassy rather than shrubby understory (Fitzgerald, et al., 2000). It can also be found in urban parks and wooded residential areas (Johnsgard, 1979) and along forest edges (Tekiela, 2001). Red-headed Woodpeckers depend on trees for nest sites, using cavities in isolated, often dead trees (Johnsgard, 1979; Busby & Zimmerman, 2001). In the tallgrass region of eastern Kansas, this species occurs more frequently in gallery forest than in attenuated gallery forest (Zimmerman, 1993).

Species-Disturbance Relationships

The effect of burning on individual grassland bird species depends on species traits, drought status, type and size of grassland, and range management, including grazing regime and the spatial and temporal scale of the burning (e.g., Zimmerman, 1992, 1997, Herkert 1994a; Herkert, et al., 1996; Walk & Warner, 2000; Fuhlendorf, et al., 2006; Askins, et al., 2007; With, et al., 2008; Grant, et al., 2010). In general, avian response to burning and subsequent succession falls into one of three categories: 1) species that colonize burned areas immediately, such as Killdeer (*Charadrius vociferous*) or Upland Sandpiper; 2) species that use sites two or more years after burning, but before woody encroachment, such as Henslow's Sparrow

(*Ammodramus henslowii*) or Grasshopper Sparrow, and 3) species that require some woody vegetation and extended protection from disturbance, such as Bell's Vireo, Brown Thrasher (*Toxostoma rufum*), or Common Yellowthroat (*Geothlypsis trichas*) (e.g., Herkert, 1994a; Fitzgerald, et al., 2000; Brawn, et al., 2001; Fuhlendorf, et al., 2006; Askins, et al., 2007; Coppedge, et al., 2008; Roberts, et al., 2012). By reducing vegetation density and removing standing dead vegetation and litter, burning, grazing and mowing can change grassland habitat suitability, at least until vegetation recovers (Zimmerman, 1992). Grassland bird diversity and abundance generally decline with increasing fire frequency and subsequent habitat homogenization (Zimmerman, 1997; Collins & Steinauer, 1998; Reinking, 2005).

The effect of burning may also depend on the type of grassland burned. For example, Walk and Warner (2000) found that avian abundance was lowest on recently burned cool season grass, but in a study of prairie wetlands, Hands (2007) found that the effect of fire frequency on abundance and species diversity was inconsistent among years. Robel, et al., (1998) found many more nests in unburned than burned fields (372 to 27), but little difference in nest success. Ground nests are vulnerable to fire regardless of its intensity, but late nesting birds such as the Field Sparrow or birds that will re-nest such as the Greater Prairie Chicken (*Tympanuchus cupido*), may not be as negatively impacted by spring burning (Best, 1979; Reinking, 2005). In general, cavity nesters respond more positively to prescribed burning than open cup or ground nesters (Saab & Powell, 2005); however, prescribed burning may still negatively impact cavity-nesting birds such as the Red-headed Woodpecker because the dead trees they prefer for nesting burn more quickly than live trees (Best, 1979).

The focal species for this study differ in their response to burning and fire frequency. Zimmerman (1993) found that in Kansas the relative abundance of Dickcissel, Eastern

Meadowlark, and Grasshopper Sparrow was not significantly different between unburned and annual burned watersheds. However, Powell (2006) found that Dickcissel were least abundant or absent at sites during the breeding season that immediately followed spring burning and Powell and Busby (2013) found that abundance was higher in unburned and idle plots. Other studies have shown that Eastern Meadowlark abundance was lower in burned or burned and grazed sites than in undisturbed prairie (Rohrbaugh, et al., 1999, Powell, 2006; Powell and Busby, 2013). Grasshopper Sparrows are uncommon on grasslands burned in the previous year (Powell, 2006), preferring to use sites after vegetation has recovered, but before woody encroachment has begun (Brawn, et al., 2001, Swengel & Swengel, 2001; Powell, 2006, 2008). Upland Sandpipers have been found to be most abundant in recently burned sites with short vegetation where foraging is more successful but litter is sufficient for nest sites (Brawn, et al., 2001; Fuhlendorf, et al., 2006; Powell, 2006, 2008; Powell & Busby, 2013; Sandercock, et al., 2015). Because it results in a more heterogeneous habitat, patch burn grazing has been found to be beneficial for species like the Eastern Meadowlark (Fuhlendorf, et al., 2006; Powell, 2006), but less so for the Dickcissel, Grasshopper Sparrow, and Brown-headed Cowbird, which were found to be more abundant in traditionally managed grasslands (Fuhlendorf, et al., 2006; Coppedge, et al., 2008; Holcomb, et al., 2014).

For Brown-headed Cowbirds, a finding of no significant difference in mean relative abundance between annually burned versus unburned plots (Zimmerman, 1993) could be because of the difference in habitat types this species uses for egg-laying compared to that used for foraging (Powell, 2006). The lower total abundance of female Brown-headed Cowbirds in the breeding season following a burn may reflect a reduction in the availability of grassland hosts more than changes in habitat suitability (Powell, 2006). In the Flint Hills, the Bell's Vireo is a

common host species for Brown-headed Cowbirds. Studies have found Bell's Vireo to be least abundant or absent in the breeding season following a burn; abundance was lowest in annually burned sites and highest in grasslands with a four-year burn cycle (Powell, 2006; 2008). Field Sparrows, like Bell's Vireo in their dependence on woody vegetation for suitable habitat, are also generally absent from annually burned grasslands (Zimmerman, 1993). Burning is tolerated where woody vegetation is thinned or prevented from encroaching, but not where it is removed entirely (Herkert, et al., 1994a, Dechant, et al., 1999b).

II. Model Variables

Species

For this study, annual bird species count data for 2000-2010 was downloaded from the USGS Patuxent Wildlife Research Center BBS website (Pardieck, et al., 2017) for seven routes: Ellinor (#38017), Lapland (#38004), Lincolnville (#38311), Longton (#38105), Olsburg (#38318), Reece (#38303), and Wreford (#38016). All routes lie within the Eastern Tallgrass Prairie, Bird Conservation Region 22 (NABCI, 2016). In Kansas, the valid survey date range is from May 25-July 7 (USGS, 2015). The earliest acceptable survey date for routes used in this study occurred on May 29 in 2000 on Longton and again in 2008 on Lincolnville. The latest acceptable survey date occurred on July 7 in 2002 on Longton and in 2008 on Lapland. Four annual surveys, 2003 and 2006 on the Lapland route and 2004 and 2006 on Longton, were conducted outside the acceptable survey date window and so were excluded from further analysis. Another four annual surveys were conducted by a first-time observer; in 2002 on Lincolnville, in 2000 on Olsburg, and in 2000 and 2007 on Reece, and so count data from these annual routes were also rejected. Not all routes were surveyed in every year, so the final number

of acceptable annual counts varied for each route: Ellinor and Wreford each had eleven years of data; Longton had nine; Lincolnville and Olsburg each had eight; and Reece had seven. Reece had both the fewest number of annual surveys and the longest gap between surveys (four years). A single observer surveyed both Lapland and Longton routes, with annual surveys for each conducted on different days. A summary of route statistics is presented in Table 2. Route statistics for all annual surveys examined are presented in Appendix 1.

TABLE 2: Summary of BBS route statistics

Route Name	Route ID	Start Latitude	Start Longitude	First Year	Years Run	Average S*	Average N^
Ellinor	38017	38.3623234	-96.5605733	1967	49	49	403
Lapland	38004	37.9847547	-96.3936159	1974	41	45	559
Lincolnville	38311	38.5224225	-96.9117521	2002	15	60	1010
Longton	38105	37.3003447	-96.1012279	1976	41	47	527
Olsburg	38318	39.6529209	-96.5297375	2000	13	74	804
Reece	38303	37.7958024	-96.4347911	2000	15	58	743
Wreford	38016	38.9939527	-96.9002609	1967	49	68	1334

*Average route species richness over the study period

^ Average route abundance over the study period

Once acceptable routes were determined, annual surveys in which the focal species route abundance was zero were removed and the abundance data from all non-zero annual routes pooled across all years. Stop abundance data for each species were converted to a binominal response variable, indicating whether that particular species was present (1) or absent (0) at that stop. As with other species distribution studies based on occurrence, 'absent' can be described more precisely as 'presumed absent' or 'undetected', and so stops could also include individuals present, but undiscovered. Counts at the same stop between years were treated as independent, although this may not be strictly true for strongly philopatric or resident species, such as the Carolina Wren (Poole, 2005).

Explanatory route variables for individual models included the route year (*Year*), survey day of the year number (*Day*), stop location in UTM coordinates for latitude (*X1*) and longitude (*Y2*), wind speed codes (USG, 2015) representing wind speed at the start and end of each survey (*StartWind*, *EndWind*), and observer code (*Observer*). Two additional predictor variables were derived, one for the length of time in hours needed to complete the route survey (*RteHours*) and the second to represent the portion of the route on which the stop in question occurred (*RTEsection*). This variable was created by dividing the route into ten sections, starting with the first stop, and assigning to each of the consecutive fifty stops a number corresponding to the section in which it occurred, thus giving a rough approximation of how close to dawn the stop was tallied. Although neither nest success nor interspecies relationships were explicitly modeled, nest parasitism by Brown-headed Cowbird could negatively impact the host species and so a variable indicating the relative abundance of the cowbird (*BCHOrelN*) was added to all models except its own. Group models included additional functional trait variables, identifying each species in terms of nest location (*NestSite*), breeding season foraging method and location (*Strategy* and *Substrate*), breeding season diet (*Diet*), and migratory pattern (*Migration*); functional trait designations were obtained from various sources including Johnsgard (1979), Vickery, et al. (1999), De Graaf, et al. (1985), Busby and Zimmerman (2001), Tekiela (2001), and Poole (2005).

Landscape

Land cover data were derived from the 2005 Kansas Land Cover Patterns—Level IV map (KARS, 2008; Peterson, et al., 2010) and used to characterize the landscape within 400m of each BBS stop, a distance consistent with BBS protocol as the limit of visual and audible detection of

species by a stationary individual (Robbins, et al., 1986). All geoprocessing operations were performed in ArcGIS, version 10 (ESRI, 2011). Explanatory landcover variables were created representing the proportional cover within each stop buffer of: *Corn*, *Sorghum*, *Soybeans, and Wheat*, with dryland and irrigated categories combined within each crop type; *AllCrops* (the four crop variables combined with 'fallow' and 'double crop' classes); *Alfalfa*; *CRP* (land enrolled in the Conservation Reserve Program, as of 2005); *WarmGrass* (warm-season, 'native' grassland); *CoolGrass* (cool-season, 'cultivated' grassland); *Water*, *Woodland*; and *WoodEdge* (calculated as the total length of the woodland edge within the buffered area). Alfalfa was included as a separate variable because birds that commonly nest in these hayfields (e.g. Eastern Meadowlark, Dickcissel, and Grasshopper Sparrow) face drastic changes in habitat structure and vegetation density when the alfalfa is mowed; the first of multiple cuttings often begins in April-May and can destroy nests, eggs, and adult birds (Frawley & Best, 1991). Native grass may also be mowed, but usually only once and not until mid-July, when most grassland birds will have made at least one nesting attempt (With, et al., 2008). Hay fields can attract high densities of nesting birds and yield high reproductive success, but early cutting can result in a population sink, especially for species that won't re-nest (Rahmig et al., 2008, With, et al., 2008).

Because they were minimally represented throughout the study area, 'Developed', 'Seasonal Emergent Wetlands', and 'Other' land cover classes were combined into a single variable (*AllElse*). In addition, all warm-season, cool-season, and CRP grasslands areas were combined to create a variable representing the core habitat (*CoreHab)* for grassland birds. To further define core habitat and reflect the potential influence of the perimeter-grassland area ratio for edge sensitive species, a variable representing the interior core habitat was created by buffering *CoreHab* by 50m and calculating the area of the interior portion (*CH_Inter50*). A

variable for the area of the largest core habitat patch (*CH_maxpch*) was also derived. Finally, a variable to represent habitat heterogeneity was created by calculating the Shannon Entropy Index for cover types within the stop buffer (*LULC_H*).

Terrain within each buffer was represented by six variables: mean elevation (*MeanElev*); mean slope (*MeanSlope*); standardized deviation of the slope (*SDslope*) to represent topographic roughness; the elevation relief ratio (*ERR30*) calculated as (Zmean-Zmin)/(Zmax-Zmin) as a different measure of local terrain relief; and the topographic slope position (*SlopePosNdx*) of the stop (Jenness, 2006), which reflects whether the site is located in an upland (positive values), valley (negative values), or an area that is flat or with an even slope (near zero values). Elevation and slope variables were calculated using a 10m digital elevation model (DEM), and the slope position index and the two topographic relief variables were based on a 30m DEM. As an index of site exposure, a transformed aspect (*TRASP*) variable was also derived, wherein the circular aspect value is reassigned to a continuous value between 0 (for north-northwest facing slopes, which are typically cooler and wetter) and 1 (for sites facing south-southwest and so hotter and more arid) (Roberts & Cooper, 1989).

Climate

Climate variables were derived using weather data available online from the PRISM (Parameter Regression of Independent Slope Model) Climate Group (PRISM, 2015) and from the National Climatic Data Center (NCDC). Variables were selected to represent annual trends, seasonality, and extreme or potentially environmentally limiting conditions that might affect reproductive success or over-wintering survival or impact vegetative conditions leading into the breeding season. Climate variables were calculated for each model year (*y*). Annual

precipitation was represented both as total annual precipitation, January 1 to December 31 (*Pann_tot*) and total precipitation for the "water year" (*Pwatyr_tot*), which represents surface water conditions and is defined by the USGS as the total precipitation for a 12-month period from October 1 in a given year through September 30 of the following year. The water year date is the ending year for the time period.

To represent seasonal conditions and extremes, a set of temperature and precipitation variables was calculated for three time periods: winter (*Win*, December (*y*-1) through February); spring (*Spg*, March through May); and summer (*Smr*, June through August). For each time season, climate variables included the mean daily maximum, mean daily mean, and mean daily minimum temperatures (e.g., *SpgTmax*, *SpgTmean*, *SpgTmin*) and the total and standard deviation of seasonal precipitation (e.g. *Pspg_tot*, *Pspg_sd*). The standard deviation of precipitation was chosen to reflect the presence of extreme precipitation events. Three variables were used to represent extreme weather conditions: number of spring days where the daily minimum temperature fell below freezing (0°C), (*SpgTmin0*); number of summer days where the daily maximum temperature exceeded 35°C (*SmrTmax35*); and the number of winter days where the daily mean temperature was below freezing (*WinTmin0*).

Finally, drought tolerance likely influences local grassland bird assemblages (Wiens, 1974a). To characterize drought conditions, variables were included for the yearly average Palmer Drought Severity Index (PDSI, Palmer, 1965) for the model year (*avgPDSI_y*) and the two previous years (*avgPDSI_y1, avgPDSI_y2*). Because March soil moisture has been correlated with total bird abundance in both burned and unburned tallgrass prairie (Zimmerman, 1992), three variables were derived for this single month for: the Palmer moisture anomaly index (Z-Index), averaged for the month of March in the model year (*ZNDX_Mar*); total March

precipitation, calculated as a percentage of the 30-year normal precipitation (*PMar_pctn*); and standard precipitation of March precipitation (*PMar_sd*). In addition, to represent drought conditions in the breeding season, a Standardized Precipitation Index (SPI, McKee, 1993) was calculated for the a six-month period leading into each of the peak breeding season months, April, May, June, and July (*SPI06_Apr*, *SPI06_May*, *SPI06_June*, *SPI06_July*).

Disturbance

Disturbance covariates were derived from the 2000-2010 fire history maps created by Rhett Mohler (2011). Mohler developed a method to map prescribed spring burning in the Flint Hills of Kansas and Oklahoma based on satellite imagery (TM and MODIS) and in situ spectrometry. Mohler mapped the cumulative number of burns (0-11) over the study period and identified the grassland acreage burned or not burned in each year. In Kansas, the majority of prescribed burns occurred in April, but the proportion of total area burned varied between years, ranging from a high of 48% in 2005 to a low of 15% in 2007 (Mohler & Goodin, 2012). Of the 81% of all grasslands in the study area burned at least once over the study period, 15% was burned only once and just 1% was burned annually. To derive the burn history variables for each model year, the area burned was first intersected with core habitat, and then the percentage of grassland area burned within each buffer was calculated for the model year (*Burn_Yr*) as well as for the two previous years (*Burn_Yr1*, *Burn_Yr2*). The suite of all variables describing route, landscape, climate, drought, and disturbance, along with their definitions, are listed in Table 3.

TABLE 3: Variables used to model species occurrence

NAME	DESCRIPTION
Route	
BHCOrelN	relative abundance of the Brown-headed Cowbird recorded at a stop
Day	survey day of the year (1-365)
EndWind	wind speed indicator for conditions recorded at the end of an annual survey. Based on the Beaufort wind force scale, which connects wind speed to observed conditions. 6 levels, from 0 (smoke rises vertically) to 5 (small trees in leaf sway)
Observer	BBS observer number for a route
RTEhours	length of time in hours and minutes needed to complete the survey
RTEsection	reflects the approximate location of a stop along a route. Values range from 1-10, with 5 stops within each section. Lower numbers indicate a stop closer to the beginning of the route (at 30 min prior to dawn)
StartWind	wind speed indicator for conditions recorded at the start of an annual survey. Based on the Beaufort scale (see EndWind), 6 levels, from 0-5
X1	stop location—longitude in UTN coordinates
Y2	stop location—latitude in UTM coordinates
Landcover	
Alfalfa	proportional cover within a stop buffer of alfalfa, including both dryland and irrigated fields
All Crops	proportional cover within a stop buffer of all cropland (includes Corn, Sorghum, Soybean, and Wheat, plus 'fallow' and 'double crop' classes)
All Else	proportional cover within a stop buffer of 'developed', 'seasonal emergent wetlands' and 'other' classes
Corn	proportional cover within a stop buffer of corn, including both dryland and irrigated fields
LULC_H	Shannon Entropy Index for landcover within a stop buffer, used as a measure of habitat heterogeneity
Sorghum	proportional cover within a stop buffer of sorghum, including both dryland and irrigated fields
Soybeans	proportional cover within a stop buffer of soybeans, including both dryland and irrigated fields
Water	proportional cover within a stop buffer of water
Wheat	proportional cover within a stop buffer of wheat, including both dryland and irrigated fields
Woodland	proportional cover within a stop buffer of woodland
WoodEdge	total length in meters of woodland edge within the buffer interior; does not include buffer edge

Landcover: Grassland	
CH_maxpch	area (m^2) of the largest core habitat (CoreHab) patch
CH_Inter50	total area (m^2) of core habitat interior, calculated by buffering by 50m each core habitat patch within a stop buffer
CoolGrass	proportional cover within a stop buffer of cool-season, 'cultivated' grasslands
CoreHab	proportional cover within a stop buffer of all warm and cool season grasslands and CRP
CRP	proportional cover within a stop buffer of grasslands enrolled in the Conservation Reserve Program, as of 2005
WarmGrass	proportional cover within a stop buffer of warm-season, 'native' grasslands
Land Surface	
ERR30	elevation relief ratio as a measure of local topographic relief calculated as (Zmean-Zmin)/(Zmax-Zmin), based on a 30m digital elevation model (DEM)
MeanElev	mean elevation within a stop buffer, based on a10m DEM
MeanSlope	mean slope within a stop buffer, based on a 10m DEM
SDslope	standard deviation of slope within a stop buffer, representing topographic roughness, based on a 30m DEM
SlopePosNdx	mean topographic slope position, representing relative stop location—in an upland area (positive value), valley (negative value), or flat or evenly sloped area (near zero values), based on a 30m DEM
TRASP	aspect transformed to have values between 0-1, where values near 0 represent north-northwest facing slopes, and values near 1, represent south-southwest facing slopes
Disturbance	
Burn_Yr	percentage of grassland area within a buffer burned in the spring of the model year
Burn_Yr1	percentage of grassland area within a buffer burned in the spring prior to the model year
Burn_Yr2	percentage of grassland area within a buffer burned in the spring t two years prior to the model year
Climate	
Seasonal time periods:	spring (spg): March-May summer (smr): June-August winter (win): December (year-1)-February
Pann_tot	total annual precipitation (ml), from Jan. 1-Dec. 31 in the model year
Pann_watyr	total precipitation (ml), from Oct 1 in the previous year through September 30 in the model year, represents surface water conditions

Pspg_tot	total precipitation (ml) for the spring
Pspg_sd	standard deviation of spring precipitation, to represent extreme precipitation events
Psmr_tot	total precipitation (ml) in the summer
Psmr_sd	standard deviation of summer precipitation, to represent extreme precipitation events
Pwin_tot	total precipitation (ml) for the winter
Pwin_sd	standard deviation of winter precipitation, to represent extreme precipitation events
SpgTmax	mean daily maximum temperature in the spring °C
SpgTmean	mean daily mean temperature in the spring °C
SpgTmin	mean daily minimum temperature in the spring °C
SmrTmax	mean daily maximum temperature in the summer °C
SmrTmean	mean daily mean temperature in the summer °C
SmrTmin	mean daily minimum temperature in the summer °C
WinTmax	mean daily maximum temperature in the winter °C
WinTmean	mean daily mean temperature in the winter °C
WinTmin	mean daily minimum temperature in the winter °C
Weather Extremes	
SpgTmin0	number of spring days were the daily minimum temperature was below 0°C
SmrTmax35	number of days summer days where the daily mean temperature was above 35°C
WinTmin0	number of winter days where the daily mean temperature was below 0°C
Drought	
avgPDSI_y	yearly average Palmer Drought Severity Index (PDSI) for the model year
avgPDSI_y1	yearly average PDSI for the year prior to the model year
avgPDSI_y2	yearly average PDSI for two years prior to the model year
PMar_pctn	total precipitation in March of the model year, calculated as a percentage of the 30-year normal precipitation
PMar_sd	standard deviation of total precipitation in March of the model year
SPI06_Apr	Standardized Precipitation Index (SPI) for a six-month period, to represent drought conditions leading into the peak breeding season month of April in the model year
SPI06_May	Standardized Precipitation Index (SPI) for a six-month period, to represent drought conditions leading into the peak breeding season month of May of the model year
SPI06_June	Standardized Precipitation Index (SPI) for a six-month period, to represent drought conditions leading into the peak breeding season month of June in the model year

SPI06_July	Standardized Precipitation Index (SPI) for a six-month period, to represent drought conditions leading into the peak breeding season month of July in the model year
ZNDX_Mar	Palmer moisture anomaly index (Z-Index), averaged for the month of March in the model year
Spatial Autocorrelation	
RACvect	probability of observing a species at one sample point conditional on its presence at neighboring points

III. Method

For each focal species, count data from all acceptable routes were combined into a single data set. The full data set for each individual species was randomly subdivided into three subsets for model training (50%), validation (25%), and testing (25%). The total number of available records varied for each species modeled, which can strongly influence model performance even with careful calibration (Elith, et al., 2008). The Brown-headed Cowbird, Dickcissel, Eastern Meadowlark, Mourning Dove, Northern Bobwhite, Red-winged Blackbird, and Yellow-billed Cuckoo had the most records, with 3100 each; Western Meadowlark had the fewest, with 1300 records, followed by Carolina Wren, with 2150 records. Unlike the other focal species, the Western Meadowlark was only present on three routes during the study period: Lincolnville, Olsburg, and Wreford. Dickcissel had the largest total abundance (5945) and stop presence (2362) over the study period, whereas the Red-headed Woodpecker had the smallest total abundance (137) and stop presence (124). For most species, the count data used were sparse and some data subsets were relatively small (400 records), so repeated 10- cross-validation (CV) was used for model calibration (i.e. training), validation, and testing (Hastie, et al., 2009).

BRT models were fitted in R (R Core Development Team, 2006) using packages *gbm*, version 2.1.1 (Ridgeway, 2015); *vegan*, version 2.4-2 (Oksanen, et al., 2017); and *dismo*, version

1.1-1 (Hijmans, et al., 2016); supplemented with custom scripts available online and developed for modeling ecological data (Elith, et al. 2008). In addition, several additional packages in R were used for graphing, statistical tests, and data exploration, including: *epi*, version 2.1 (Carstensen, et al., 2017), *ncf*, version 1.1-7 (Bjornstad, 2016), *raster*, version 2.5-8 (Hijmans, 2016), *spdep*, version 0.6-8 (Bivand, et al., 2013; Bivand & Piras, 2015) and *ROCR*, version 3.3.2 (Sing, et al., 2005). All BRT models were fitted using a Bernoulli loss function, a bag fraction (***bf***) of 0.625, the default step size of 50 trees per iteration, and 20,000 as the maximum number of trees. Following guidelines suggested by Elith et al. (2008), all final models were also required to generate at least 1000 trees. Other metaparameter settings were calibrated for each species separately, because what constitutes 'optimal' may vary with prevalence; for instance, very common or very rare species may require a slower ***lr*** given the same sample size (Elith et al., 2008).

Models were evaluated for fit and predictive performance based on values generated by the CV process within the *gbm* package; final fitted values for each model are calculated within the program as the sum of results for all individual trees, multiplied by the learning rate (De'ath, 2007; Elith, et al., 2008), and include the residual and total mean deviance, as well as the mean estimated CV holdout residual deviance (CV deviance) and a value for the area under curve (AUC) of the Receiver-Operating-Characteristic (ROC). Deviance measures how well the response variable is predicted by the candidate model, with a reduced set of predictor variables, compared to the prediction by a saturated model, which has as many parameters as observations. Since deviance measures misclassification error, a smaller number is preferred. In addition to these performance measures, a *pseudo* R^2, or D^2 score, where D^2 = (mean total deviance-mean residual deviance)/mean total deviance), was calculated for each final fitted model to aid in

selecting the 'best' model formula and to compare final model results between species and habitat specificity groups. A D^2 score describes how much of the total mean deviance is accounted for by the fitted model. Since all models have the same number of variables, an adjusted D^2 was not used.

For each species, model calibration involved first creating a single decision stump model (two terminal nodes) using the training data set and running a model with a ***tc*** of 1, an ***lr*** of 0.01, and all 65 predictors. Subsequent trials with the same training data set involved testing a combination of seven tree complexity levels (***tc***=2,3,4,5,6,7,10) and at least seven consecutive learning rates (***lr*** range=0.01, 0.0075, 0.005, 0.0025, 0.001, 0.00075, 0.0005, 0.00025, 0.0001) and all predictors. Once all possible ***tc*** and ***lr*** combinations were explored, the top three best performing combinations were each run again five times on the training data set and the results averaged. The metaparameter combination (i.e. model formula) resulting in the best fit based on average CV deviance, ROC score, and D^2 was then used to run a new set of models using the validation data and the full set of 65 variables (base model). Validation base models were repeated 20 times and the final fitted values averaged. All base models were then refit using an autocovariate term, defined as the probability of observing a species at one sample point conditional on its presence at neighboring points within certain distance classes (Augustin, et al., 1996; Coppedge, et al., 2004; Dormann, et al., 2007, 2012).

Using a simplification process described by Elith, et al. (2008) that is similar to backward selection in regression, redundant or uninformative variables were removed from the base model by dropping the least important variable and refitting the model. This process was repeated until only the top 30 most influential predictor variables for each species remained. The simplified model was then run 20 times and the CV results averaged. Even where the presence of RAC in

the base model was indicated by the Moran's I result, the autocovariate term was not always retained as a variable of influence during subsequent simplification of each model. The metaparameters selection, autocovariate, and simplification procedures were repeated for the obligate, facultative, and shrub-woodland group models; however the same model formula (***tc***=5, ***lr***=0.005, ***bf***=0.625) for was used for all groups.

To evaluate how well the validation models performed when applied to new data, the individual model formula for each species was applied against the corresponding test data set that had been withheld from model development. In addition to reporting the final fitted values, relative influence plots were created to provide a visual comparison of relative variable influence between species. Relative influence reflects the number of times that variable is selected for splitting, weighted by the squared improvement at each split, averaged over all trees, and expressed as a percentage (Elith, et al., 2008). Finally, partial dependence plots were calculated, showing the marginal effect of an explanatory variable on the response variable when the values of all other variables are held at their mean (Elith, et al., 2008). Variable interactions can also be investigated using two-way joint partial dependence plots; however, many of the top variable interactions in this study included a categorical variable, which cannot be plotted in this manner, and so these plots were not explored further.

IV. Results

A summary of model fit and performance results is presented in Table 4, with model parameters and full results listed in Appendix 2. In all cases, simplified models outperformed models using the full set of variables (base models) in terms of CV deviance, ROC score, and deviance explained by the model (D^2 score). CV deviance measures the mean residual deviance

TABLE 4: Summary of the model performance for focal species BRT models.

Species (AOU Code)	CV deviance (SE)	ROC score (SE)	Pseudo R^2
Bell's Vireo (BEVI)			
Simplified Model	0.439 (0.02)	0.725 (0.04)	8.082
Test Model	0.406	0.698	4.514
Brown-headed Cowbird (BHCO)			
Simplified Model	1.152 (0.07)	0.758 (0.02)	15.815
Test Model	1.250	0.704	9.160
Carolina Wren (CARW)			
Simplified Model	0.587 (0.02)	0.743 (0.03)	9.991
Test Model	0.563	0.720	9.041
Common Nighthawk (CONI)			
Simplified Model	0.524 (0.03)	0.824 (0.03)	21.424
Test Model	0.550	0.828	23.129
Dickcissel (DICK)			
Simplified Model	0.839 (0.03)	0.806 (0.02)	20.310
Test Model	0.876	0.819	19.873
Eastern Meadowlark (EAME)			
Simplified Model	1.066 (0.03)	0.812 (0.02)	23.128
Test Model	1.046	0.802	24.539
Field Sparrow (FISP)			
Simplified Model	0.657 (0.02)	0.781 (0.03)	17.346
Test Model	0.569	0.820	14.795
Grasshopper Sparrow (GRSP)			
Simplified Model	0.882 (0.04)	0.819 (0.02)	23.902
Test Model	0.917	0.802	20.640
Mourning Dove (MODO)			
Simplified Model	1.180 (0.03)	0.745 (0.02)	13.733
Test Model	1.265	0.690	7.922
Northern Bobwhite (NOBO)			
Simplified Model	1.129 (0.03)	0.771 (0.02)	16.820
Test Model	1.159	0.768	16.065
Red-headed Woodpecker (RHWO)			
Simplified Model	0.344 (0.02)	0.742 (0.04)	8.466
Test Model	0.465	0.545	-5.470
Red-winged Blackbird (RWBL)			
Simplified Model	1.081 (0.31)	0.792 (0.02)	20.128
Test Model	1.057	0.727	11.947
Upland Sandpiper (UPSA)			
Simplified Model	0.723 (0.03)	0.870 (0.01)	32.675
Test Model	0.755	0.861	27.391
Western Meadowlark (WEME)			
Simplified Model	0.420 (0.06)	0.940 (0.02)	51.118
Test Model	0.498	0.886	37.212
Yellow-Billed Cuckoo (YBCU)			
Simplified Model	0.959 (0.03)	0.773 (0.02)	14.985
Test Model	0.997	0.719	9.267

in the test subset held out for each fold in the k-fold cross validation process and is an indication of how well the proposed model would perform on an independent data set. In most cases, simplified models that allowed variable interactions had better performance in terms of CV deviance than models where interactions were not allowed. Where the single decision stump models had higher scores (Bell's Vireo, Carolina Wren, Northern Bobwhite, and Red-winged Blackbird), the difference was minimal. For consistency, all results presented here are based on simplified models.

For individual species models, CV deviance (the CV standard error follows each score) ranged from the best score of 0.344 (0.017) for Red-headed Woodpecker to the worst score of 1.180 (0.028) for Mourning Dove. CV deviance, when averaged for individual models within habitat specificity groups, was best for scrub-woodland species at 0.597 (0.023), followed by obligate species at 0.786 (0.039), and facultative species, 1.013 (0.038). Within the scrub-woodland group, the Red-headed Woodpecker model was the best performing in the group and overall. The least successful model in that group was for the Yellow-billed Cuckoo, which had a CV deviance of 0.959 (0.028). Within the obligate birds group, the best CV deviance score was 0.420 (0.058) for the Western Meadowlark; however, the BRT model for this species was unstable for unknown reasons, producing inconsistent results and occasionally giving warning messages that the model algorithm had 'failed to converge'. The reason is unclear, but one explanation could be because one or more variables predicted the response almost perfectly. The second best obligate species model was for Upland Sandpiper, with a CV deviance of 0.723 (0.034), and the least successful in the group was the Eastern Meadowlark model, with a CV deviance of 1.066 (0.034). For facultative species, the best model was for Common Nighthawk with CV deviance of 0.524 (0.029), a score that was the third best overall and substantially better

than all other facultative species. The model for the Mourning Dove had the worst CV deviance result, both within the facultative group and over all species modeled individually. When data for each habitat specificity group were combined prior to running a single group model, the order of best fit based on CV deviance was the same as when the results of individual species were averaged; the shrub-woodland group performed best, with 0.647 (0.011), followed by the obligate group, at 0.855 (0.018), and the facultative group, at 1.037 (0.013).

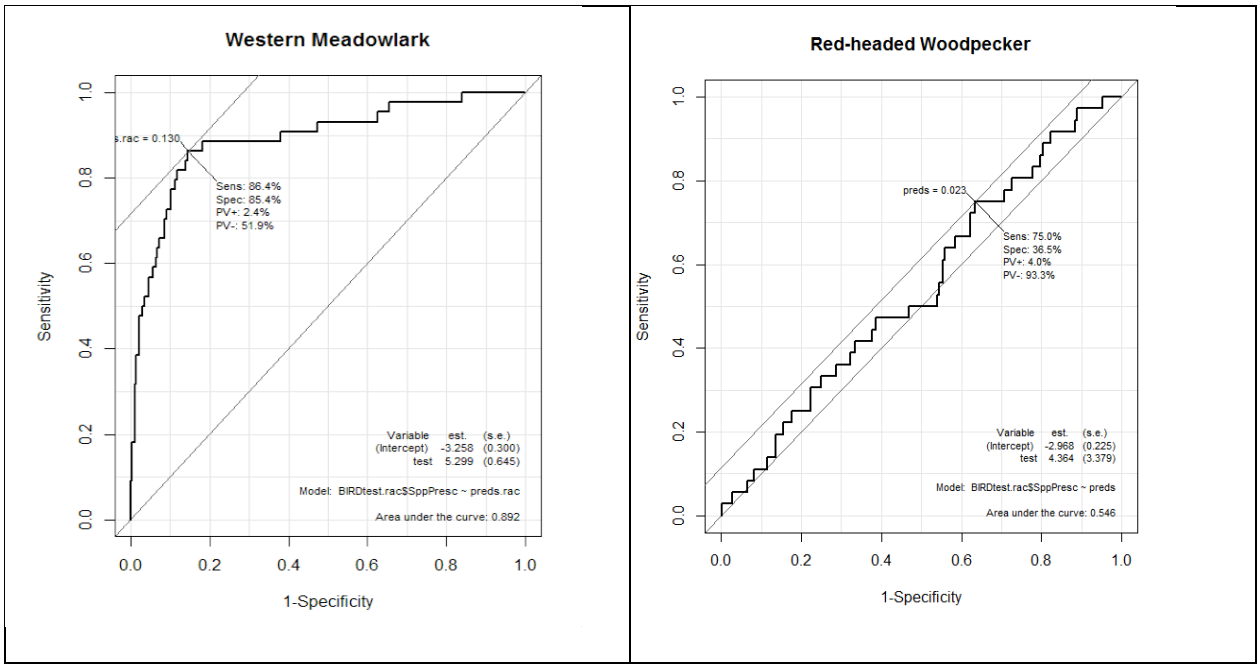
When evaluating model performance based on ROC scores (roughly comparable to a traditional academic grading system), the best average performance was by the obligate group, with a group ROC score of 0.849 (0.017). The best species model within that group, and best over all models considered individually, was for the Western Meadowlark, 0.940 (0.019); the second best model in the obligate group, for models considered individually, was for the Upland Sandpiper, 0.870 (0.014). The lowest individual model ROC score within the group, 0.806 (0.017) was for the Dickcissel model. Facultative species had the second best average ROC score of 0.778 (0.019); the best individual model within the group was for the Common Nighthawk, with a ROC score 0.824 (0.029), that was also better than three of the five obligate species. The least successful model within the facultative group was again for the Mourning Dove, with a ROC score of 0.745 (0.019). The shrub-woodland group had the lowest average ROC score, 0.752 (0.032), as well as the individual species model with the lowest ROC score overall, Bell's Vireo, at 0.719 (0.017). The Red-headed Woodpecker model had the best individual ROC score, 0.742 (0.043) in the shrub-woodland group. Single group models had the same model performance order as averaged individual species models when considering ROC scores: the obligate group model was best, with a ROC score of 0.882 (0.006), followed by the facultative group model, 0.799 (0.007), and then the shrub-woodland group, 0.766 (0.012).

Focal species models were also judged on how much the final model accounted for of the total mean deviance, expressed as D^2. Among all individual models, the highest D^2 was the Western Meadowlark, with 80.46% of total mean deviance explained by the model, followed by the Upland Sandpiper model, which explained 62.27%. The lowest D^2 was for the Mourning Dove, whose final model accounted for only 28.98% of the total mean deviance. Based on this performance statistic, the obligate group again had the best average D^2 score, 58.14%; average final model D^2 scores were similar for the shrub-woodland and facultative species groups, with final models explaining an average of 42.96% and 41.85% of total mean deviance, respectively. The obligate species with the worst model performance was the Grasshopper Sparrow, which accounted for only 46.60% of total mean deviance; however, this result was still better than the average result for both shrub-woodland and facultative groups. The order of percent deviance explained (D^2 scores) for single group models departed slightly from that for averaged results of single species models; the obligate species single model was still first, with 53.71% of the total mean deviance explained, but was followed by the facultative species single model, which explained 39.17%. The shrub-woodland group was least effective, with its single model accounting for only 30.17% of the total mean deviance.

Finally, individual species models were evaluated for their predictive performance when applied to independent data withheld from model training and validation. The Bell's Vireo model, at 0.406, had the best predictive performance based on CV deviance, followed by the Red-headed Woodpecker, at 0.465. Both species belong to the shrub-woodland group. The two models with the worst predictive performance based on CV deviance were for the Mourning Dove, at 1.265, and the Brown-headed Cowbird, at 1.250. Both are facultative species and both are relatively general in their habitat requirements. When evaluated based on ROC score,

however, the best predictive performance was found for the Western Meadowlark (0.886) and Upland Sandpiper (0.861) models and the worst was for the Red-headed Woodpecker (0.545) and Mourning Dove (0.690) models. AUCROC plots for the Western Meadowlark and Red-headed Woodpecker are shown in Figure 1; plots for all models are presented in Appendix 3. In terms of percent deviance explained (D^2) using independent data, the best test models were for the Western Meadowlark (37.21%) and Upland Sandpiper (27.39%) and the worst were for Bell's Vireo (4.51%) and Red-headed Woodpecker (-5.47%). When predictive performance results were averaged according to habitat group, shrub-woodland species had the best average CV deviance (0.600), followed by the obligate (0.818) and facultative (1.056) groups. When considering ROC score, however, obligate species had the highest average score (0.834), followed by facultative species (0.734) and shrub-woodland species (0.700).

FIGURE 1: AUCROC plots showing the best (Western Meadowlark, ROC score=0.886) and worst (Red-headed Woodpecker, ROC score= 0.545) predictive performance for focal species models applied to independent data.



Focal species models were also compared based on relative influence of predictors. The relative influence of all predictors on each simplified model is listed in Appendix 4, with the five most influential predictors for each species presented in Table 5. When a bootstrap sample of the training or validation data is used, the order of variables and the exact relative variable influence value may vary between model runs, but the difference is usually small. Relative influence represents how often a predictor is chosen for splitting, but not whether the influence is positive or negative. Examination of two-dimensional partial dependence plots is useful in clarifying the effect a single variable has on the response variable; however, strong interactions or correlation between variables can complicate interpretation (Friedman, 2002; Elith, et al., 2008). Two-dimensional partial dependence plots showing the fitted functions for five of the most influential variables in each focal species model are presented for visual comparison in Figure 2. Partial dependence plots for the fifteen most influential variables retained in each simplified model are shown in Appendix 5. A single predictor, *RTEsection*, appeared most frequently, with thirteen instances, including five as the most important explanatory variable. Following *RTEsection*, three single variables were each represented six times: *Observer*, *MeanElev*, and *CH_Inter50*. Including *RTEsection* and *Observer*, route variables accounted for a third of all top five variables, making it the most represented variable category. Landcover predictors were also important, appearing twenty-two times in the top five list; with *Core_Inter50,* nine different landcover variables were represented, four of which related to grasslands.

Terrain featured prominently in the top five list as well, with six variables appearing a total of eighteen times. Two disturbance variables, *Burn_Yr1* (four times) and *Burn_Yr2* (once)

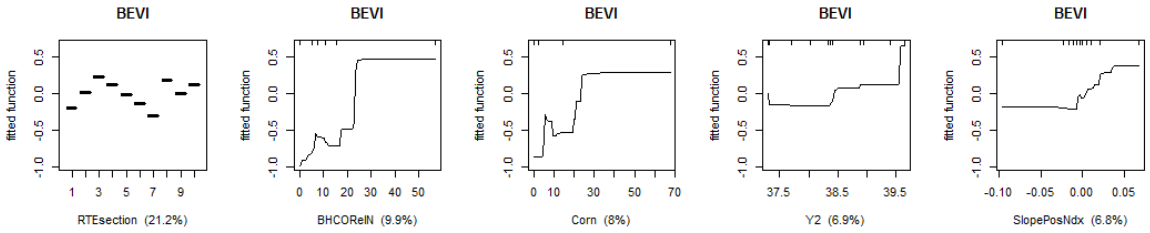
TABLE 5: Relative influence of the five most important predictors for each species model. AOU codes (Pyle & DeSante, 2014) used for species common names are listed in Table 1. Variable names are defined in Table 3.

Obligate		**Facultative**		**Shrub-Woodland**	
DICK	**rel.inf**	**BHCO**	**rel.inf**	**BEVI**	**rel.inf**
RTEsection	11.5283	RTEsection	18.4712	RTEsection	16.4131
Woodland	11.0127	Observer	16.3162	BHCOrelN	7.9399
WoodEdge	10.9466	MeanElev	11.4211	Corn	6.4771
MeanSlope	3.7835	Burn_Yr2	3.8223	SlopePosNdx	5.4162
Observer	3.3398	RteHours	3.6298	Y2	4.0649
EAME	**rel.inf**	**CONI**	**rel.inf**	**CARW**	**rel.inf**
CoreHab	9.8851	RTEsection	21.6394	WoodEdge	12.4484
CH_Inter50	9.5482	SlopePosNdx	8.2601	Pspg_sd	9.0107
RTEsection	7.3566	Burn_Yr1	7.6292	SPI06_Apr	8.1002
Observer	5.6835	CH_Inter50	6.3992	WarmGrass	6.8865
MeanElev	4.8702	MeanElev	4.8638	RTEsection	6.5612
GRSP	**rel.inf**	**MODO**	**rel.inf**	**FISP**	**rel.inf**
CH_Inter50	17.0977	X1	16.9635	RTEsection	17.5044
WarmGrass	12.7143	RTEsection	14.4413	Observer	11.6304
RTEsection	8.6245	TRASP	5.2692	MeanSlope	11.2479
Burn_Yr1	5.5624	Observer	5.2249	WarmGrass	6.3514
MeanElev	4.6504	MeanSlope	4.8956	CH_Inter50	3.5875
UPSA	**rel.inf**	**NOBO**	**rel.inf**	**RHWO**	**rel.inf**
CH_maxpch	17.9281	CoreHab	7.6583	LULC_H	12.0124
RTEsection	8.5414	RACvect	7.0688	Soybean	8.2582
MeanElev	8.2822	CH_Inter50	6.8977	RTEsection	7.1370
Burn_Yr1	6.8963	RteHours	4.9772	WinTmean0	5.0370
CH_Inter50	6.5570	Burn_Yr1	4.8179	CoreHab	4.7273
WEME	**rel.inf**	**RWBL**	**rel.inf**	**YBCU**	**rel.inf**
MeanSlope	24.7966	MeanSlope	15.2786	WoodEdge	10.4580
SDslope	13.7844	WoodEdge	8.0851	RTEsection	7.6875
RTEsection	11.4948	Woodland	8.0402	Observer	7.2022
ERR30	9.3348	TRASP	7.0313	RteHours	6.8241
MeanElev	6.1717	X1	4.8865	SlopePosNdx	5.9445

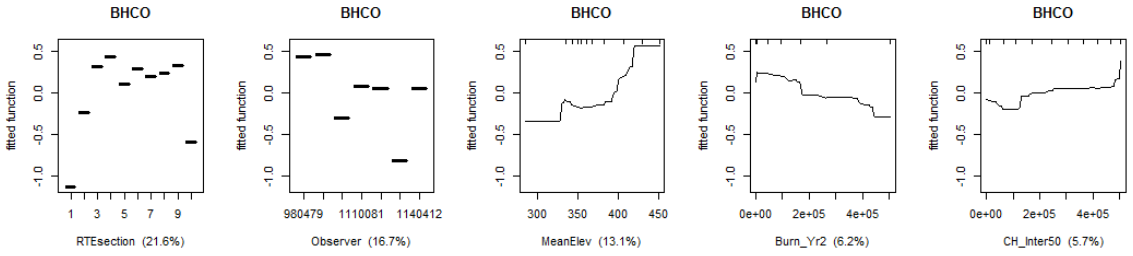
accounted for five slots in the top-five most important variables. Climate variables appeared only three times in the top-five groups; one predictor representing spring precipitation, one for spring drought conditions, and one for winter temperature extremes. The autocovariate term (*RACvect*), added to all base models but dropped from five with simplification, was counted only once in the top five group, as was the relative abundance of Brown-headed Cowbirds. For the focal species modeled in this study, the top five predictors accounted for an average of approximately 45% of the total variable influence. For obligate species, the average was slightly higher, at 48%. The top ten variables in each model accounted for an average of about 62.5 % of the total and the top fifteen variables averaged around 75%. The average influence of ten and fifteen variables was again slightly higher for obligate species, 64.5% and 76.4% respectively.

FIGURE 2. Partial Dependence Plots for the Five Most Influential Variables for each focal species model. For each variable, the partial dependence plot shows the marginal effect of that variable on the response, when the value of all other variables is averaged (Elith, et al., 2008). Fitted functions (y-axis) are on a logit scale; higher fitted function values represent a greater impact on species occurrence based on the values of that variable. Decile rug marks at the top of each plot show the distribution of sites across the range of that variable. Variable names are defined in Table 3.

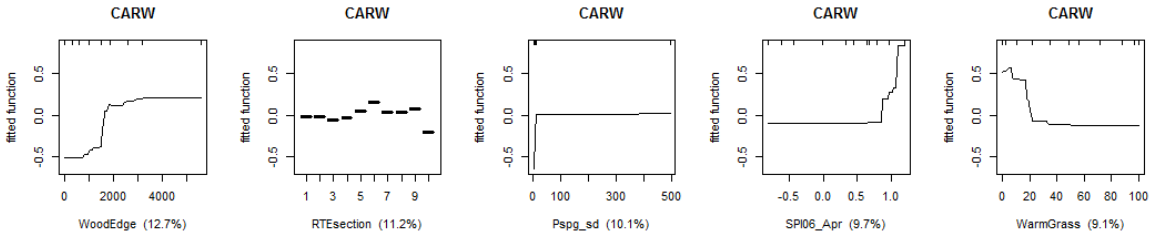
A. Bell's Vireo



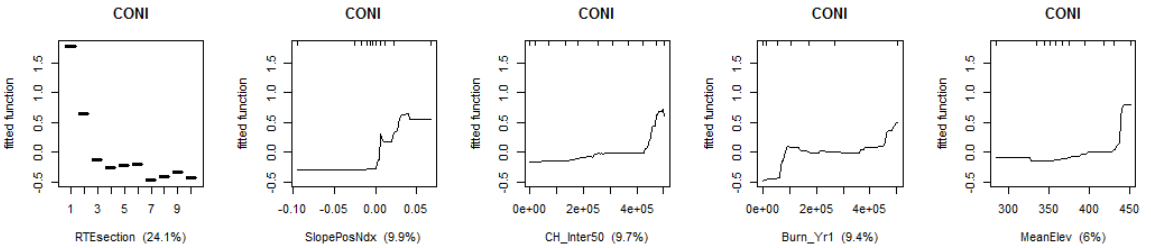
B. Brown-headed Cowbird



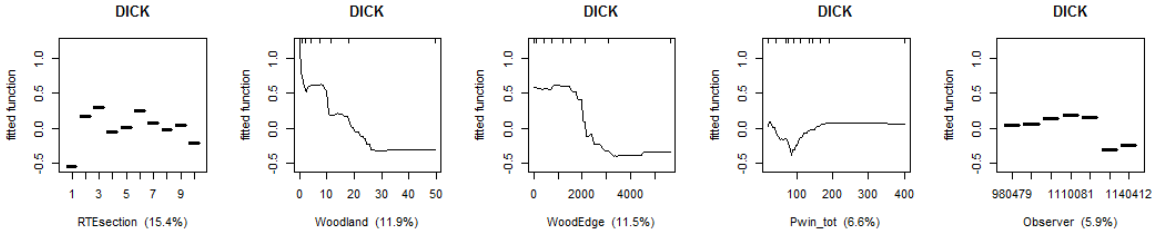
C. Carolina Wren



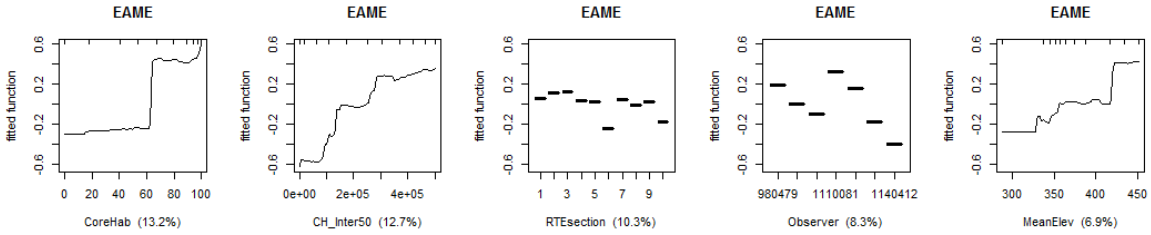
D. Common Nighthawk



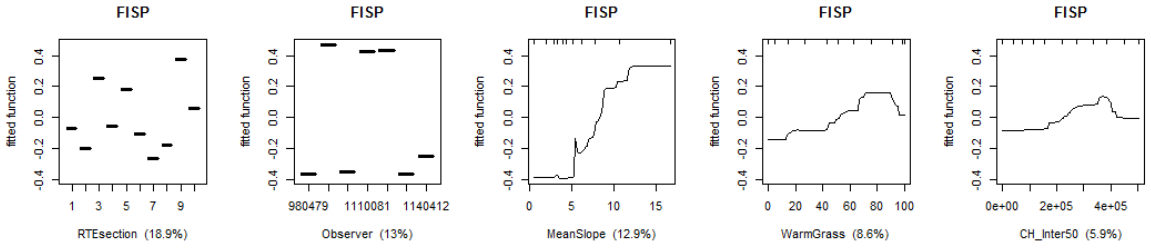
E. Dickcissel



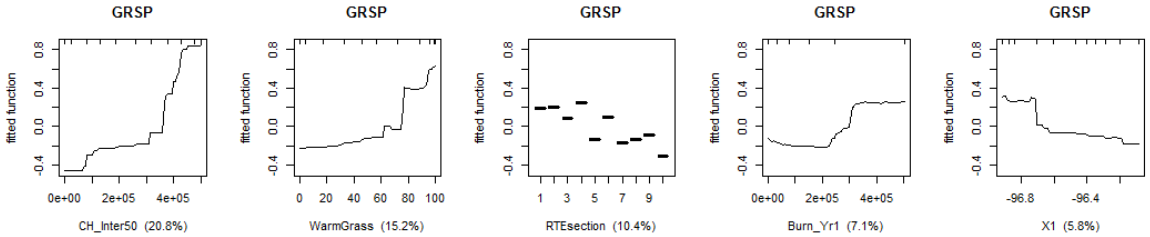
F. Eastern Meadowlark



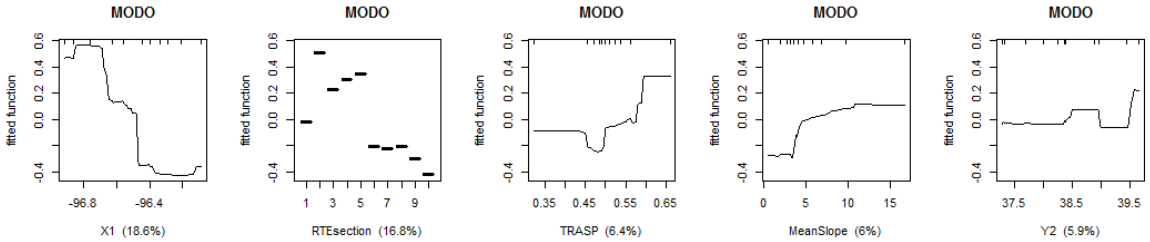
F. Field Sparrow



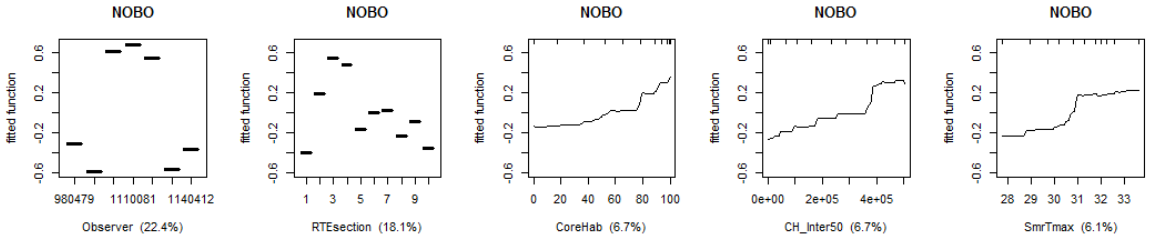
G. Grasshopper Sparrow



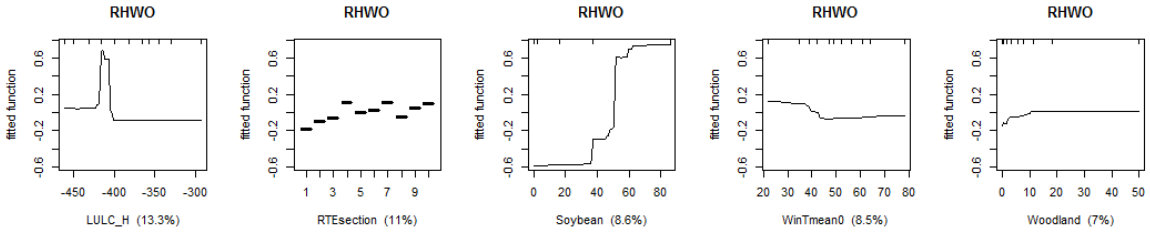
H. Mourning Dove



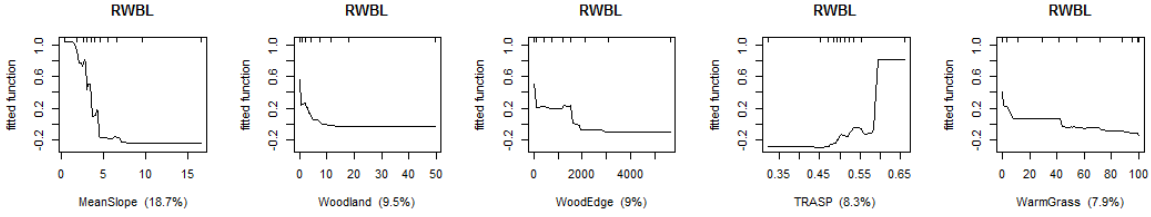
I. Northern Bobwhite



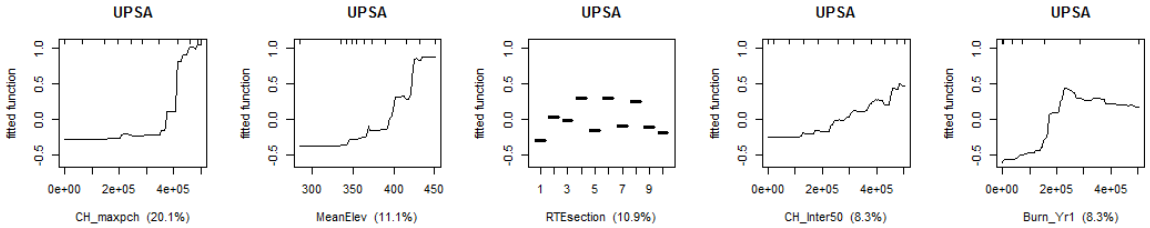
J. Red-headed Woodpecker



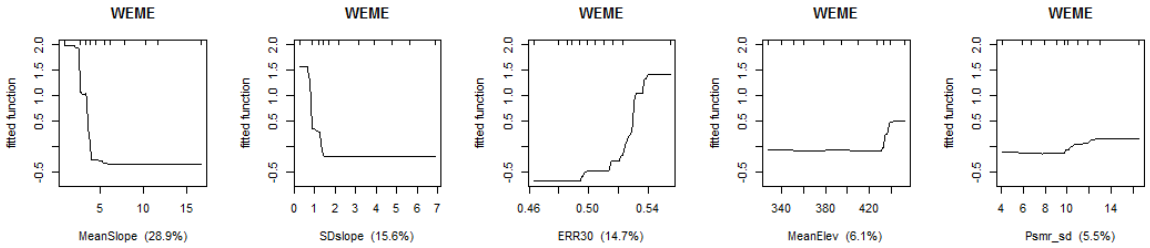
K. Red-winged Blackbird



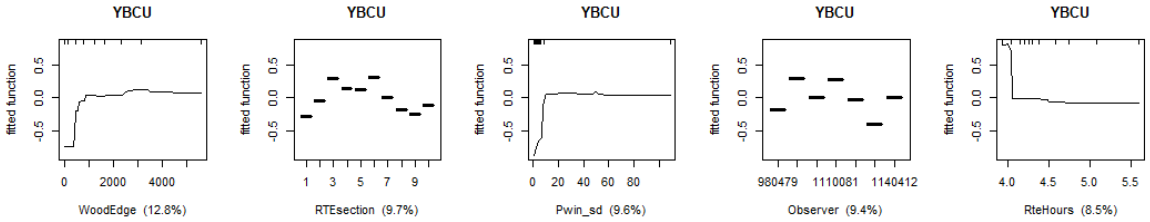
L. Upland Sandpiper



M. Western Meadowlark



N. Yellow-billed Cuckoo



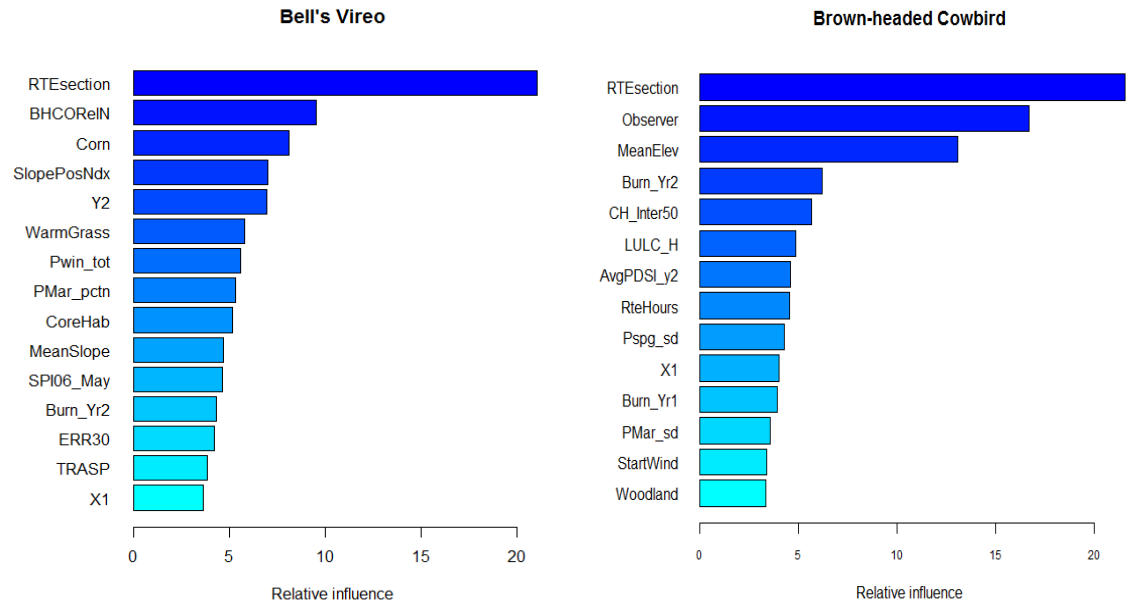
The relative variable influence plots vary in shape depending on whether the influence of predictors is evenly spread or whether a few explanatory variables dominate the model. Relative influence plots showing the top fifteen most influential variables in each species model are shown in Figure 3. Averaged across all species within the group, landcover variables were the predominant category for both obligate and shrub-woodland species as a group, whereas route variables dominated for facultative species. In all cases, the most important category of variables represented an average of about 28% of the total variable influence. Terrain variables made up the second most important category for both obligate and facultative species, accounting for about 24.5% and 22.5% of the total influence, respectively. For shrub-woodland species, terrain

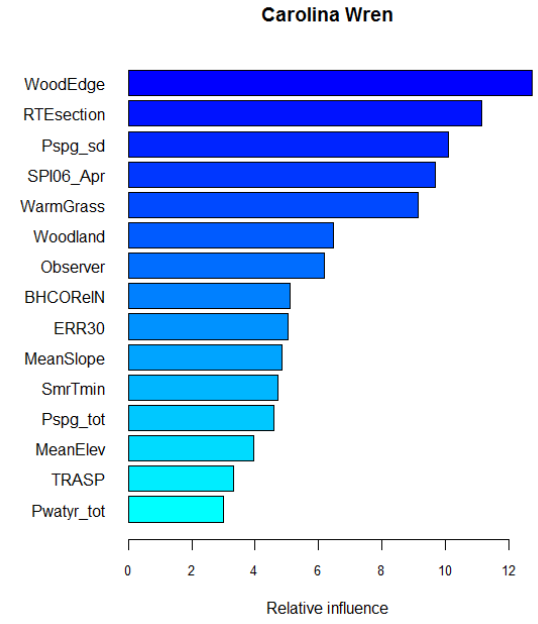
predictors accounted for less than 15% of the total variable influence and climate predictors were the second most important category with around 20.8% of total influence. Climate variables, excluding drought, were less important overall for obligate species, together representing less than 16% of total variable influence. For facultative species the total was around 19%. For all species groups, the predictor precipitation variables together were more important than those reflecting temperature. Total influence for both precipitation and temperature predictors was less than 10% in all groups except for shrub-woodland species. For those species, precipitation variables made up 12% of the total variable influence.

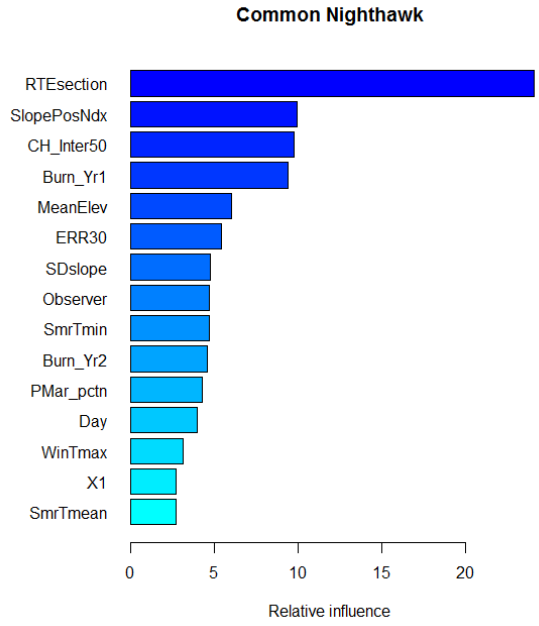
Route variables were prominent in all models, with *RTEsection* making the simplified variable set for all species except Red-winged Blackbird. Since the route section variable was designed to be a surrogate for time since the start of each survey, 30 minutes prior to daybreak, it's possible that this species is not restricted to activity early in the day. Male Red-winged Blackbirds, in particular, have a distinctive song and appearance that could make it more noticeable at all times along the route. *RTEsection* was the most important variable for five species (Dickcissel, Brown-headed Cowbird, Common Nighthawk, Bell's Vireo, and Field Sparrow), the second most important variable for three species (Upland Sandpiper, Mourning Dove, and Yellow-billed Cuckoo) and the third most important variable in four species models, the Eastern Meadowlark, Grasshopper Sparrow, Red-headed Woodpecker, and Western Meadowlark. The route variable for *Observer* was included in all simplified models except for the Bell's Vireo, Red-headed Woodpecker, Red-winged Blackbird, and Western Meadowlark; however, this variable was only in the top five most important for the Brown-headed Cowbird, Dickcissel, Eastern Meadowlark, Field Sparrow, Mourning Dove, and Yellow-billed Cuckoo models.

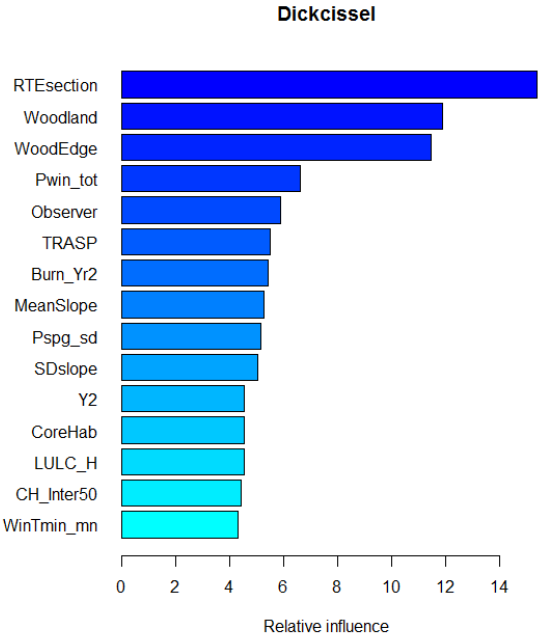
Variables for *RTEhours*, *Day*, *StartWind*, *EndWind*, Longitude (*X1*), and Latitude (*Y2*) were also retained in some simplified models. Longitude was the only location variable for five species, and for the six species models where the latitude variable was also present, longitude had greater important in four. Latitude was the only site location variable for the Dickcissel and Yellow-billed Cuckoo models. Western Meadowlark and Carolina Wren were the only two species that had no site location variables present in the final model. The autocovariate variable, *RACvect*, was present in all final models except for the Brown-headed Cowbird, Eastern Meadowlark, Mourning Dove, Western Meadowlark and Yellow-billed Cuckoo. The variable representing the relative abundance of cowbirds was retained in all final models except for Common Nighthawk, Dickcissel, Red-headed Woodpecker, and Upland Sandpiper.

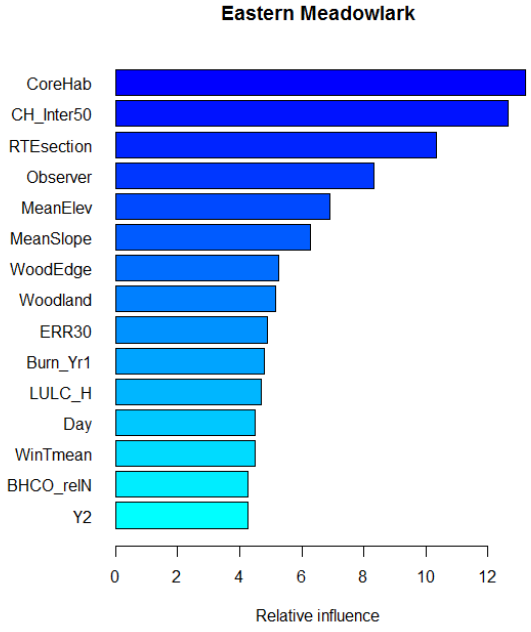
FIGURE 3: Relative variable influence plots showing the top fifteen most influential variables for each focal species. Relative variable influence reflects the number of times a variable is selected for splitting, weighted by model improvement, and averaged over all trees (Elith, et al., 2008). Variable names are defined in Table 3.

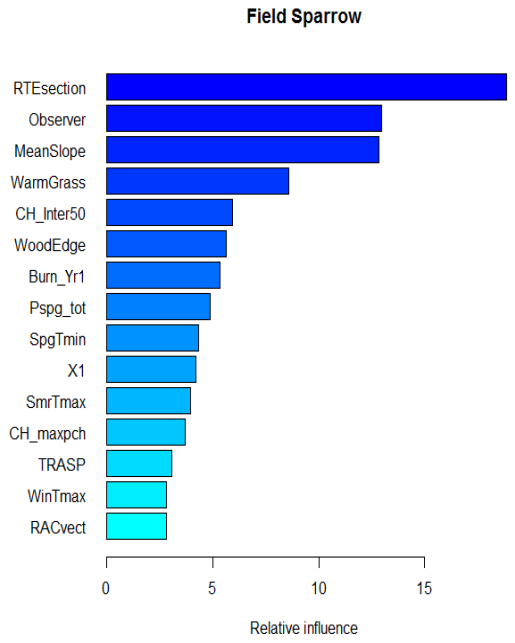


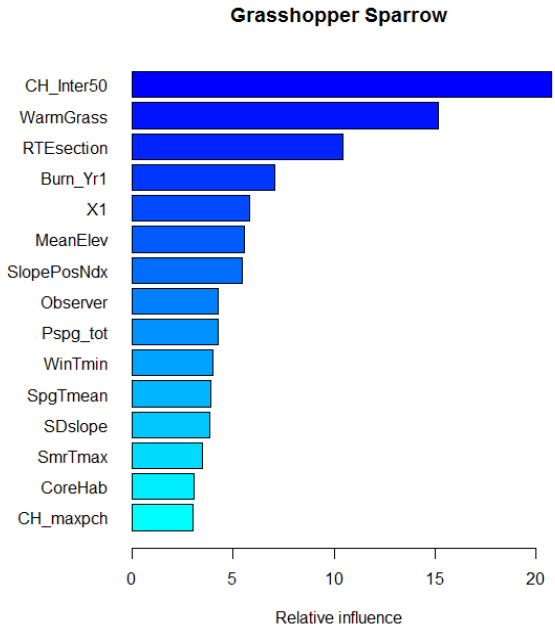

Carolina Wren
WoodEdge
RTEsection
Pspg_sd
SPI06_Apr
WarmGrass
Woodland
Observer
BHCORelN
ERR30
MeanSlope
SmrTmin
Pspg_tot
MeanElev
TRASP
Pwatyr_tot
0
2
4
6
8
10
12
Relative influence

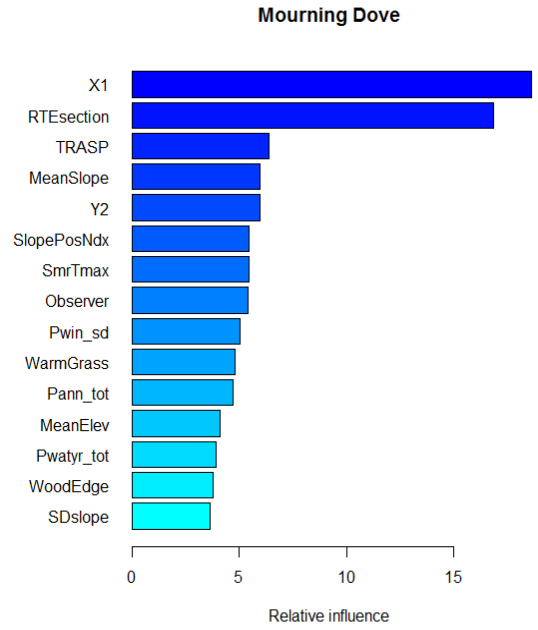

Common Nighthawk
RTEsection
SlopePosNdx
CH_Inter50
Burn_Yr1
MeanElev
ERR30
SDslope
Observer
SmrTmin
Burn_Yr2
PMar_pctn
Day
WinTmax
X1
SmrTmean
0
5
10
15
20
Relative influence

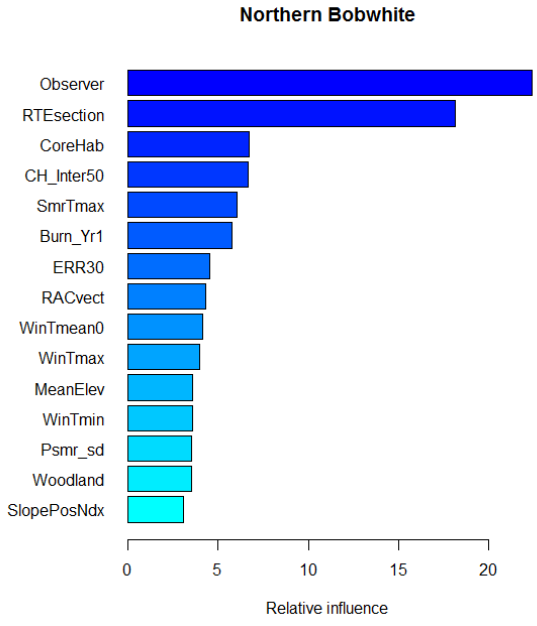

Dickcissel
RTEsection
Woodland
WoodEdge
Pwin_tot
Observer
TRASP
Burn_Yr2
MeanSlope
Pspg_sd
SDslope
Y2
CoreHab
LULC_H
CH_Inter50
WinTmin_mn
0
2
4
6
8
10
12
14
Relative influence

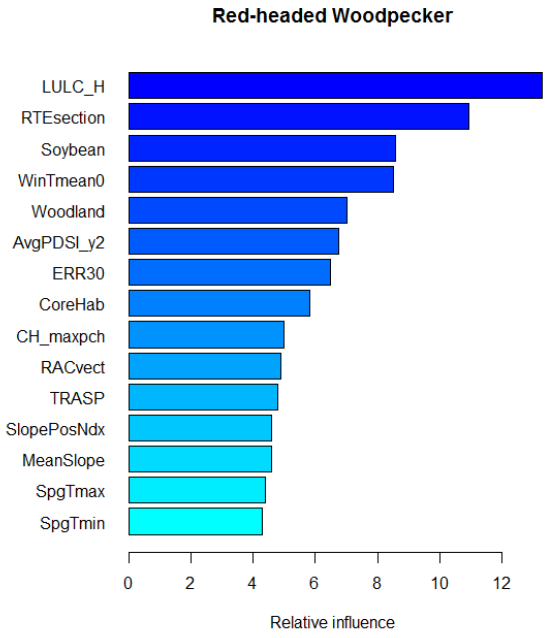

Eastern Meadowlark
CoreHab
CH_Inter50
RTEsection
Observer
MeanElev
MeanSlope
WoodEdge
Woodland
ERR30
Burn_Yr1
LULC_H
Day
WinTmean
BHCO_relN
Y2
0
2
4
6
8
10
12
Relative influence

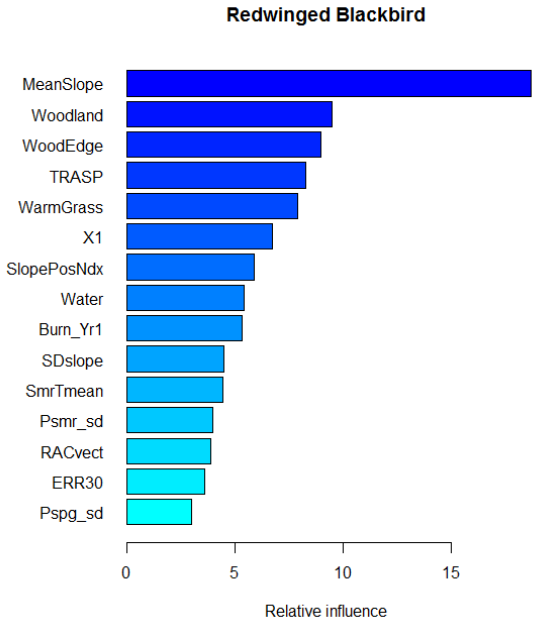

Field Sparrow
RTEsection
Observer
MeanSlope
WarmGrass
CH_Inter50
WoodEdge
Burn_Yr1
Pspg_tot
SpgTmin
X1
SmrTmax
CH_maxpch
TRASP
WinTmax
RACvect
0
5
10
15
Relative influence

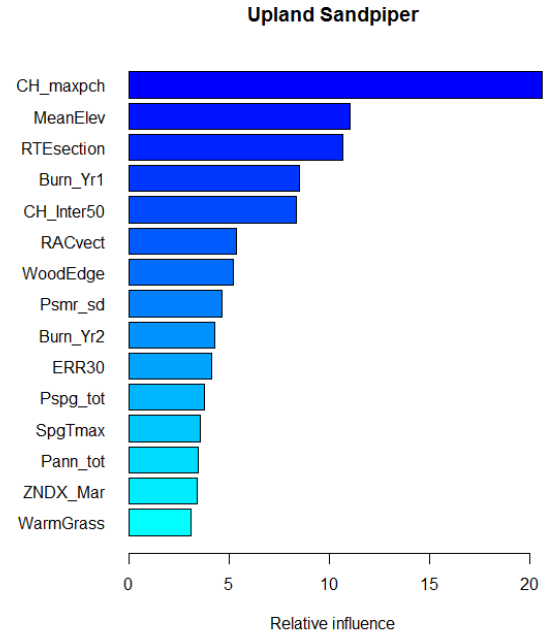

Grasshopper Sparrow
CH_Inter50
WarmGrass
RTEsection
Burn_Yr1
X1
MeanElev
SlopePosNdx
Observer
Pspg_tot
WinTmin
SpgTmean
SDslope
SmrTmax
CoreHab
CH_maxpch
0
5
10
15
20
Relative influence

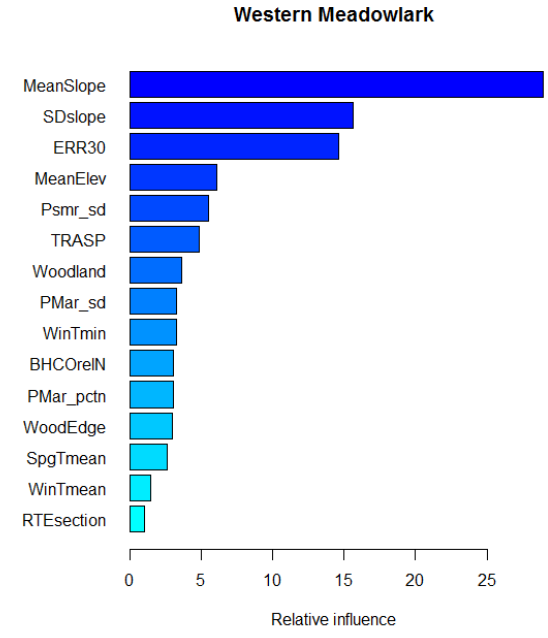

Mourning Dove
X1
RTEsection
TRASP
MeanSlope
Y2
SlopePosNdx
SmrTmax
Observer
Pwin_sd
WarmGrass
Pann_tot
MeanElev
Pwatyr_tot
WoodEdge
SDslope
0
5
10
15
Relative influence

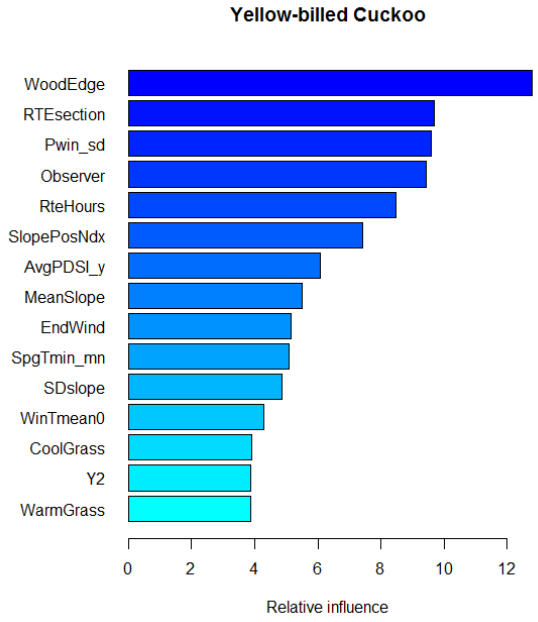

Northern Bobwhite
Observer
RTEsection
CoreHab
CH_Inter50
SmrTmax
Burn_Yr1
ERR30
RACvect
WinTmean0
WinTmax
MeanElev
WinTmin
Psmr_sd
Woodland
SlopePosNdx
0
5
10
15
20
Relative influence


Red-headed Woodpecker
LULC_H
RTEsection
Soybean
WinTmean0
Woodland
AvgPDSI_y2
ERR30
CoreHab
CH_maxpch
RACvect
TRASP
SlopePosNdx
MeanSlope
SpgTmax
SpgTmin
0
2
4
6
8
10
12
Relative influence


Redwinged Blackbird
MeanSlope
Woodland
WoodEdge
TRASP
WarmGrass
X1
SlopePosNdx
Water
Burn_Yr1
SDslope
SmrTmean
Psmr_sd
RACvect
ERR30
Pspg_sd
0
5
10
15
Relative influence


Upland Sandpiper
CH_maxpch
MeanElev
RTEsection
Burn_Yr1
CH_Inter50
RACvect
WoodEdge
Psmr_sd
Burn_Yr2
ERR30
Pspg_tot
SpgTmax
Pann_tot
ZNDX_Mar
WarmGrass
0
5
10
15
20
Relative influence


Western Meadowlark
MeanSlope
SDslope
ERR30
MeanElev
Psmr_sd
TRASP
Woodland
PMar_sd
WinTmin
BHCOrelN
PMar_pctn
WoodEdge
SpgTmean
WinTmean
RTEsection
0
5
10
15
20
25
Relative influence



Excepting *CRP*, which was included only in the final models for Bell's Vireo and Field Sparrow, two or more grassland variables were present in the final model for every species. *CoreHab* was included in all models except Bell's Vireo. *CoolGrass* was the least prevalent grassland variable with lowest average influence, but was still included in eight models; *WarmGrass* was included in two additional models, and had an average variable influence value almost twice as high. Both habitat 'patch' variables, *CH_maxpch* and *CH_Inter50*, were included in eleven species models, with both variables included in all obligate species models. Not surprisingly, the average influence value of all grass categories combined, was almost twice as high for obligate species as for both other groups. The Grasshopper Sparrow had the highest total relative influence value for combined grassland variables (almost 34.5%), with two predictors, *CH_Inter50* and *WarmGrass*, accounting for three-quarters of the total amount. The Dickcissel model was unusual in having less than ten percent of total relative variable influence

represented by grass categories. After *RTEsection*, the second and third most influential variables in the Dickcissel model were *Woodland* and *WoodEdge*, comprising nearly 22% of the total relative influence and representing the highest relative influence value for both variables among all other models.

Precipitation and temperature variables occurred in all individual species models; taken together they averaged 18.15% in total variable influence. Except for Common Nighthawk, Grasshopper Sparrow, Northern Bobwhite, and Red-winged Blackbird, total relative variable influence for precipitation was greater than that for temperature. March precipitation variables, either *Mar_pctn* or *Mar_sd* or both, were included in all species models except Grasshopper Sparrow, Mourning Dove, Red-Winged Blackbird, and Carolina Wren. The standard deviation of summer precipitation (*Psmr_sd*) occurred most frequently (ten models), followed by *Mar_pctn* (nine models). All seasonal temperature variables appeared in focal species models. Mean daily maximum winter temperature (*WinTmax*) was the most frequently included temperature variable and mean daily minimum temperature (*WinTmin*) was the least common. Temperature variables were represented fairly evenly across seasons.

Variables reflecting seasonal low temperature extremes in winter (*WinTmean0*) and spring (*SpgTmin0*) were retained in seven models; however, the variable for summer high temperature extremes was dropped from all base models when simplified. *WinTmean0* was included in models for four resident or probable resident species and one migrant species. *SpgTmin0* was included in two resident or probable resident species and two migrant species. The final models for Red-headed Woodpecker and Yellow-billed Cuckoo included both variables. Eleven of fifteen species models retained at least one variable reflecting drought; five of the eleven models had two drought variables in the final model and all shrub-woodland

models had at least one. The SPI variables for April (three models) and May (one model) were included in final models, but SPI variables for March and June were dropped from all models. The *ZNDX_Mar* variable, representing short-term drought in March only, was included in models for Common Nighthawk, Red-winged Blackbird, and Upland Sandpiper. The three variables representing drought over a longer term, *AvgPDSI_y, AvgPDSI_y1,* and *AvgPDSI_y2,* were included in five models.

All models included at least one burn history variable; the combined total of all variables present in a model averaged 5.42% of the total relative influence. The largest combined burn total was 12.23% for Upland Sandpiper; the second highest, 11.15%, was for the Common Nighthawk. The smallest combined burn variable total was for Western Meadowlark, with 1.26%; the Carolina Wren model had the second smallest total with 2.59%. The single burn variable with the greatest variable influence across all species was for the Common Nighthawk model, with 6.90% relative variable influence for burning in the prior year to the model year (*Burn_yr1*). The variable for burns in the same model year (*Burn_yr*) was included in only five models, but the *Burn_yr1* predictor was present in all models except Bell's Vireo. The variable for burns two years prior to the model year (*Burn_yr2*) occurred in all but three final models, Western Meadowlark, Red-winged Blackbird, and Yellow-billed Cuckoo. Three species models had a single burn variable represented; *Burn_yr1* for Western Meadowlark and Red-winged Blackbird, and *Burn_yr2* for Bell's Vireo. Four final models, Grasshopper Sparrow, Field Sparrow, Mourning Dove, and Upland Sandpiper, included all burn variables. Eight final models included both *Burn_yr1* and *Burn_yr2* predictors, but only the final model for the Yellow-billed Cuckoo included *Burn_yr* and *Burn_yr1*.

V. Discussion

Model performance can be tied both to individual species abundance and relative prevalence, as well as to the inclusion of appropriate environmental predictors that capture both broad and narrow aspects impacting habitat use. For instance, the models for species where data was sparse, such as for the Bell's Vireo and Red-headed Woodpecker, were on the whole less successful based on percent deviance explained or ROC score than models for species that were more abundant and more prevalent, such as for the Dickcissel or Eastern Meadowlark. Specificity of habitat requirements can also impact how well a species distribution model works. For example, the model for the Mourning Dove, a facultative grassland species with relatively general habitat requirements, was less successful than that of the Upland Sandpiper, an obligate species with more specific habitat needs.

Model performance can also be negatively impacted when the ratio of predictors to observations is large, when strongly correlated variables are included, or when a few attributes dominate all others in terms of predictive power. In this study, a larger suite of explanatory variables was initially considered and strongly correlated variables (Spearman's *rho* >0.7) were removed prior to initial model training. An additional variable for the relative stop abundance of the focal species perfectly predicted the response and was also removed prior to training. Despite using a reduced set of predictors, the final number of predictors used was still relatively large. For the Western Meadowlark model, this issue was compounded because this species occurred on only three routes and thus had far fewer observations than other models, resulting in an even larger predictor to record ratio. In addition, this model was dominated by a few relatively highly correlated variables representing several aspects of terrain. While the model was among the best in terms of model performance and predictive power, warning messages that

the model algorithm had 'failed to converge' were often generated, even when trial runs were made without the dominant variables.

Including irrelevant variables or omitting key environmental predictors can also reduce model performance. In this study, at least one variable was included that may not have performed as expected and so could have biased model results. *RTEsection* figured prominently among the five most influential variables. This variable was intended to represent time since the survey start, 30 minutes prior to dawn, thereby revealing the influence of the proverbial 'dawn chorus', a period of heightened bird activity in the early morning. For the single crepuscular species, the Common Nighthawk, this variable seemed to work as anticipated, as demonstrated by the partial dependence plot for *RTEsection* showing the fitted function to be highest in the first route section and falling off sharply thereafter. Models for several other species, such as the Grasshopper Sparrow, Mourning Dove, and Northern Bobwhite, demonstrated a similar, albeit not so extreme, pattern relating higher occurrence with early route sections. However, *RTEsection* may have inadvertently captured the influence of terrain and available habitat along the route, as evidenced by the scattered or distinctly non-monotonic response to this variable in models for species such as Bell's Vireo and Field Sparrow.

Similarly, *Observer* was included as a variable because observer biases in BBS count data are well recognized (e.g., Link & Sauer, 1998; O'Connor, et al., 2000). Fitted functions with high values for some observers could well reflect a difference in observer skill for species such as the Field Sparrow, which are sensitive to human activity and display subtly colored plumage. However, in this study, the "observer effect" could also represent a disparity in preferred habitat for a particular species between routes. Terrain variables may also reflect the influence of landcover more than just the impact of landscape position. For example, in the Flint

Hills lower elevations may be stream drainages, with a greater proportion of trees, or a flatter floodplain area, with a greater proportion of cropland. In contrast, a higher mean elevation likely represents an upland area with more grass and less woody vegetation. Areas of rough terrain or steep slopes may also have more woody vegetation, with copses of shrubby trees along small drainages and rocky outcrops.

The relative influence of predictors can be explained based in part on the functional traits and habitat preferences of the particular species being modeled. Not surprisingly, landcover variables representing different aspects of grasslands had greater total influence for obligate grassland species than for the other groups, most likely because obligate species are more restricted in their habitat requirements. With the exception of Western Meadowlark, all obligate species models had grassland variables in the top fifteen most influential predictors. Only the Western Meadowlark model failed to retain any grassland variables within the top fifteen most important, and the Dickcissel model had none within in the top five. For the Western Meadowlark model, the dominance of terrain predictors representing slope, elevation, and terrain relief seem to show a habitat preference for flatter, upland areas, which may be more xeric with shorter, sparser grass. In the Dickcissel model, the relative influence of *Woodland* and *WoodEdge* is greater than for any grassland variable, but examination of the partial dependence plots for these variables reveals that this result likely represents an avoidance of smaller habitat patches rather than a preference for woody vegetation. The variable *CH_Inter50* appeared most frequently among the most influential grassland variables. This result is not surprising considering that most of the obligate species modeled prefer larger patches, with a smaller perimeter to area ratio.

For facultative and shrub-woodland species models, landcover variables as a whole were important, but less so than for obligate species models. For facultative species models, this probably reflects the more flexible grassland habitat requirements of the species modeled. All facultative species models retained at least one grassland variable within the fifteen most important. Not surprisingly, the grassland variables were ranked highest in models for facultative species with more specific habitat requirements (Northern Bobwhite and Common Nighthawk). The Brown-headed Cowbird model had the most grassland variables, which could reflect the preferred habitat of its grassland bird host species. *WoodEdge* was also retained in the simplified model for this species, but its relative influence was much less. For shrub-woodland species models, landscape variables collectively were less important than in obligate species models possibly because only two variables were used to describe woody vegetation, versus six variables for grassland cover. Three shrub-woodland species models retained both woody vegetation variables. *WoodEdge* was retained in the Bell's Vireo simplified model, which matches this species' preference for more shrubby, low canopy vegetation. In the Red-headed Woodpecker simplified model, the *Woodland* variable was retained, reflecting this species' preference for open forest.

Of particular interest in this study was the impact of burning on grassland bird occurrence. In the final species models, the three burn variables were retained a total of 31 times. The variable that represents burning in the model year (*Burn_Yr*) was retained in models for the Grasshopper Sparrow, Field Sparrow, Mourning Dove, Upland Sandpiper, and Yellow-billed Cuckoo. Only in the Mourning Dove model was this variable the most influential of the three burn variables retained; however, the relative influence for the three burn variables retained was less than two percent each, and the only positive influence on occurrence was with an

increase in the area burned in the prior year. Considering that the Common Nighthawk nests on bare ground, it seems surprising that burning in the model year was a variable not retained in the simplified model for this species. However, this species model had the highest relative influence value for any single burn variable (*Burn_Yr1*) and the highest total relative influence for combined burn variables, except for the Upland Sandpiper model, which retained all three burn variables instead of only two. The variable for burning in the prior year (*Burn_Yr1*) was retained in simplified models more than any other burn variable, appearing a total of fourteen times, including four times in the top five most influential variables. This variable also had the highest total relative influence (47.14%) across all models, more than the other two variables combined. The variable for burning two years prior to the model year (*Burn_Yr2*) was retained in twelve models, but had a total relative influence across these models of less than thirty-one percent. While the results indicate that burning in the prior year is the most important burn variable affecting habitat occupancy for most of the species modeled, interpretation of the real impact of any burning is complicated by the lack of information regarding other range management aspects, such as mowing or grazing pressure, that could impact habitat use.

When all burn variable results within a habitat group are combined, the average relative influence was highest for the facultative group; however, this finding is likely skewed by the results from several species models. For instance, in the obligate species group, the models for the Dickcissel and Western Meadowlark were dominated by three non-grassland variables, accounting for between 33-50% of total relative influence for each species. Although the Upland Sandpiper model accounted for the greatest total relative influence for burn variables, it is not enough to make up for the low totals represented in the other two models, particularly in the Western Meadowlark model, which had the lowest total relative influence for burn variables

among all species models. In addition to the lower than expected total relative influence for burn variables for these two obligate species models, the model for the Common Nighthawk had a total relative influence for burn variables nearly twice as high as any other facultative species. While this result makes sense for the individual species, it does skew the group average.

CHAPTER 3: AVIAN ASSEMBLAGE STRUCTURE

Abstract

In this study, the impact of prescribed spring burning on the diversity and structure of grassland bird communities in the Flint Hills of Kansas was investigated for the 2000-2010 breeding seasons. For each study year, sites were categorized based on the presence of burning in the spring of that breeding season. Diversity between burn groups was evaluated using a selection of diversity indices commonly used in ecological studies. The magnitude of difference in mean diversity index values was used to assess the strength of any difference in diversity found between burned versus unburned sites. The similarity of avian communities between and within these burn groups was evaluated using paired distance matrices correlating geographic distance and assemblage structure. The statistical significance of differences in community similarity between and within burn groups was evaluated using nonparametric analysis of variance and visualized through ordination nonmetric multidimensional scaling.

I. Background

Prescribed range burning is a common practice throughout much of the Great Plains region, including the Flint Hills region, and is used to improve cattle forage by stimulating the growth of new grasses, eliminating standing dead vegetation, and reducing litter depth, and also to suppress the encroachment of woody vegetation (Smith & Owensby, 1972; Knopf & Samson, 1997; Briggs, et al., 2002, 2005; Reinking, 2005). Traditional methods of range management in the Kansas tallgrass prairie region call for extensive annual burning coupled with moderate to intensive grazing pressure. This combination of burning and grazing results in a homogenous

landscape of low vegetation over large areas (Fuhlendorf, et al., 2006). Patch burn grazing is a relatively recent alternative to large-scale annual burning and intensive stocking (Fuhlendorf & Engle, 2001). With this approach, rangeland is burned in smaller sections over the course of successive years and cattle are allowed free access to patches that vary in time since burning (Vinton, et al., 1993; Coppedge & Shaw, 1998; Fuhlendorf & Engle, 2001; Coppedge, et al., 2008; Fuhlendorf, et al., 2009; Allred, et al., 2011). Patch burn grazing results in a more heterogeneous landscape, with patches of taller grass, deeper litter, standing dead vegetation, and some woody vegetation (Fuhlendorf & Engle, 2001, 2004; Fuhlendorf, et al., 2006, 2009). This more structurally complex habitat ensures a diversity of locally available niches and positively impacts local bird abundance and community composition (MacArthur & MacArthur, 1961; MacArthur, et al., 1962; Wiens, 1973, 1974b; Rotenberry & Wiens, 1980; Cody, 1981; Zimmerman, 1992, 1997; Patterson & Best, 1996; Roth, 1976; Anderson, 2006). To maintain a mosaic of habitat types, burning small tracts successively at a three to five year interval is recommended (Zimmerman, 1988; Herkert, et al., 1996; Fitzgerald, et al., 2000; Vickery, et al., 2000; Powell & Busby, 2013).

In the Flint Hills, planned grassland burns are conducted most often in the spring (Mohler & Goodwin, 2012), at a time when many grassland birds are selecting their home range and establishing territories (Swengel & Swengel, 2001; Sandercock, et al., 2015). In this study, the grassland bird community response to spring burning was examined to determine whether diversity and assemblage structure differed in sites that were burned in the spring of the breeding season year compared to sites that were unburned. Changes in community structure as a result of disturbance can be expressed as changes in species richness, abundance, evenness, dominance and/or community similarity, but evenness has been found to change more quickly than richness

in response to disturbance (Dornelas, et al., 2011). Evenness reflects how equally the number of individuals in an assemblage is spread among the species present, which in effect, describes the variance in relative abundance. An assemblage dominated by a few common (abundant) species or many rare species is uneven; nearly all communities are naturally highly uneven (Maurer & McGill, 2011). Where two assemblages have the same number of species, the community with greater evenness is considered more diverse (Hillebrande, et al., 2008; Maurer & McGill, 2011).

Because the various diversity indices emphasize different aspects of a community, such as the number of rare or common species, they act as complementary rather than redundant measures (Magurran, 2011; Legendre & Legendre, 2012). The choice of metrics used to describe diversity is a tradeoff between sensitivity, generality, and interpretability. Diversity and similarity metrics are nonparametric and usually normally distributed; however, they are impacted by differences in sampling effort, including sampling duration, interval, number of samples, etc. (Gotelli & Colwell, 2001; Palmer, et al., 2007; Jost, et al., 2011; Magurran, 2011; Maurer & McGill, 2011). To minimize differences in sampling effort and perhaps more realistically represent differences in diversity, indices used in this study were converted to Hill numbers, or the "effective number of species present" (MacArthur, 1965; Hill, 1973: 427). The effective number of species is defined as the number of equally common species necessary to produce a given diversity value, and is said to reflect the "true diversity" of a community (Hill, 1973; Jost, 2006). Diversity indices converted in this way are essentially in the same units and so direct comparisons can be made without introducing artifacts unrelated to real trends (Gotelli & Colwell, 2001; Jost, 2006).

The effect of burning on individual grassland bird species and grassland bird communities depends in part on species traits, but also on the type and size of grassland, plus the

fire's extent, severity, season, and the grazing regime that follows (e.g., Zimmerman 1992, 1997; Herkert 1994a; Herkert, et al., 1996; Walk & Warner, 2000; Fuhlendorf, et al., 2006; Askins, et al., 2007; With, et al., 2008; Grant, et al., 2010). In grasslands, avian species richness has been found to vary depending on time since burning, being lowest in the first post-burn growing season, but returning to pre-burn status within two to three years (Zimmerman, 1992; Robel, et al., 1998; Swengel & Swengel, 2001; Coppedge, et al., 2008; Grant, et al., 2010; Roberts, et al., 2012). The assemblage shift is transitory, however, because birds occupy adjacent unburned habitat rather than disappear completely (Grant, et al., 2010). Frequent burning has been found to decrease bird species diversity by eliminating shrub/wood dependent species and reducing the abundance of other species (Zimmerman, 1992). Powell & Busby (2013) found that species richness, evenness, and diversity were similar between burned and unburned sites, but overall abundance was highest in unburned idle parcels and lowest on recently burned idle parcels. They concluded that no combination of treatments (burned, unburned, grazed, hayed or idle) was best or worst at attracting the highest number of every species. Robel, et al. (1998) found no statistically significant difference in species richness between burned and unburned grasslands, but mean abundance was lower where burning had occurred. Taxonomic distinctiveness has also been found to decline with increasing anthropogenic disturbance (Clarke & Warwick 1998; Schweiger, et al., 2008).

Study Area

The study area encompassed 16 counties that overlap the majority of the Kansas portion of the Flint Hills physiographic region: Butler, Chase, Chautauqua, *Coffey*, Cowley, Elk, Geary, Greenwood, Lyon, Marshall, *Marion*, Morris, Pottawatomie, Riley, Wabaunsee, and *Woodson*

(counties listed in italics are adjacent to, but not considered part of the 13 core counties of the Kansas Flint Hills region). The Flint Hills are characterized by expansive tallgrass prairies, rolling hills, steep valleys, and limestone outcroppings; upland areas have shallow, rocky soils that are more xeric and less productive than the deeper soils of the floodplains (Knapp, et al., 2002; Briggs, et al., 2005; Frey, et al., 2008). In the study area, the majority of grasslands are held in large, privately owned parcels most often used for cattle ranching (Towne & Owensby, 1984; Fitzgerald, et al., 2000). Croplands exist, but are generally restricted to lowland floodplains. Trees and shrubs occur in gallery and attenuated gallery forests along watercourses, along fencerows and in shelterbelts, in small copses associated with rocky outcroppings, and in grasslands and oldfields where burning has been suppressed. Counties along the periphery of the Flint Hills region have less total grassland area, typically occurring as smaller, more fragmented tracts interspersed with cropland (Mohler, 2011).

II. Method

Species Data

Avian population data were obtained from the North American Breeding Bird Survey (BBS), a large-scale, long-term international monitoring program administered jointly by the U.S. Geological Survey (USGS) and the Canadian Wildlife Service that was initiated in 1966 in response to concerns over pesticide effects on birds (Bystrak, 1981; Pardieck, et al., 2017). BBS is an annual roadside survey conducted during the peak nesting season for breeding birds in North America, in June for much of the continental U.S, but starting in May in desert regions and southern states and extending into July in northern states and Canada (Robbins, et al., 1986). Individual routes are 39.4 km (24.5 miles) long, with 50 stops ideally at 800m (0.5 mile)

intervals. Surveys begin 30 minutes prior to local sunrise. At each stop, an observer performs a 3-minute count, recording all birds seen or heard within a 400 m (0.25 mile) radius and noting any adverse weather conditions, traffic, or other factors that might influence counts. BBS point counts can be biased, primarily in relation to roadside sampling (e.g. Bart, et al., 1995; Griffith, et al., 2010; McCarthy, et al., 2012), imperfect detection (e.g., O'Connor, et al., 2000; Sauer, et al., 2013), and especially, observer effects (e.g., Faanes & Bystrak, 1981; Emlen & DeLong, 1992; Sauer, et al., 1994, 2013; Kendall, et al., 1996). Because the assumptions of random sampling and equal detection are not met, population estimates based on these data can be inaccurate; for diversity indices, however, ignoring detection has been found to impact the magnitude of trends, but not their direction (Buckland, et al., 2011). Despite their acknowledged flaws, these data are commonly used by conservation groups and were the only source of historical, region-wide bird population estimates available for this study.

Community structure was analyzed at the Breeding Bird Survey (BBS) stop level for the survey years 2000-2010. Annual count data were downloaded from the USGS Patuxent Wildlife Research Center BBS website (Pardiek, et al., 2017) for seven routes that lie completely within study area: Ellinor (#38017), Lapland (#38004), Lincolnville (#38311), Longton (#38105), Olsburg (#38318), Reece (#38303), and Wreford (#38016). Four annual surveys, 2003 and 2006 on the Lapland route and 2004 and 2006 on Longton, were conducted outside the acceptable survey window (in Kansas, May 25-July 7) and were excluded from further analysis. Another four annual surveys were conducted by a first-time observer; in 2002 on Lincolnville, in 2000 on Olsburg, and in 2000 and 2007 on Reece, and so count data from these annual routes were also rejected. A single annual route that was not completed was also excluded. In all, a total of 62 annual routes were deemed acceptable, with survey dates ranging from May 29 to July 7. A

summary of route statistics is listed in Table 1. Statistics for each annual survey are listed in Appendix 1.

Once satisfactory routes were determined, all species present on each route over all study years were recorded to create a route specific species list. Any species observed on three or fewer acceptable routes or with five or fewer occurrences across the study period were considered accidental or vagrant species and were removed from all species lists. Any species tallied but not identified was also excluded. To include rare species, but eliminate those suspected of being transient, analysis was restricted to species that made up at least 1% of the total abundance on any route over the study and that was tallied at least once on all seven routes examined. A single exception was made for the Western Meadowlark (*Sturnella neglecta*). This species was only present on three routes over the study period, but on those three routes was present in every year surveyed. In addition, this species had special interest as an obligate grassland species. Obligate grassland species are defined as those species entirely reliant on grasslands for all or part of their life cycle; in contrast, facultative grassland species use grasslands regularly, but not exclusively, and are capable of using a wider range of habitat types than obligate species (Vickery, et al., 1999). Because they are difficult to accurately census by BBS methods (Robbins, et al., 1986; Sauer, et al., 2013), any raptors, wading birds, or waterbirds not otherwise excluded were also removed from the final species list. Finally, sparse data for most species were expected to cause complications when calculating distance matrices, so a 'dummy' species with an abundance equal to one at every stop was added to the species data set for each year

To reduce the impact of dominant species, abundance data at each stop were transformed to relative abundance, prior to calculating indices. The final species list, with the common name

TABLE 1: Summary of BBS route statistics.

Route Name	Route ID	Start Latitude	Start Longitude	First Year	Years Run	Average S*	Average N^
Ellinor	38017	38.3623234	-96.5605733	1967	49	49	403
Lapland	38004	37.9847547	-96.3936159	1974	41	45	559
Lincolnville	38311	38.5224225	-96.9117521	2002	15	60	1010
Longton	38105	37.3003447	-96.1012279	1976	41	47	527
Olsburg	38318	39.6529209	-96.5297375	2000	13	74	804
Reece	38303	37.7958024	-96.4347911	2000	15	58	743
Wreford	38016	38.9939527	-96.9002609	1967	49	68	1334

*Average route species richness over the study period

^ Average route abundance over the study period

and American Ornithological Union (AOU) 4-letter Alpha Code (Pyle & DeSante, 2014) is summarized in Table 2. Names listed in bold are considered facultative or obligate grassland species according to Vickery, et al. (1999); hereafter grouped as *grassland* species. Species names not listed in bold are generalist species or species dependent on some degree of woody vegetation. For the purposes of this project, those species were collectively referred to as *shrub-woodland* species. The ten most abundant species over the study period were the Dickcissel (*Spiza Americana*), Eastern Meadowlark (*Sturnella magna*), Brown-headed Cowbird (*Molothrus ater*), Mourning Dove (*Zenaida macroura*), Northern Bobwhite (*Colinus virginianus*), American Crow (*Corvus brachyrhynchos*), Red-winged Blackbird (*Agelaius phoeniceus*), Upland Sandpiper (*Bartramia longicauda*), Northern Cardinal (*Cardinalis cardinalis*), and the Barn Swallow (*Hirundo rustica*); all except the American Crow, Northern Cardinal, and Barn Swallow are considered grassland obligate or facultative species. A table including species scientific names and abundances is presented in Appendix 6.

TABLE 2: Species list and AOU codes. Names in **bold** are facultative or obligate grassland species, according to Vickery, et al. (1999).

Common Name	AOUcode*	Common Name	AOUcode*
American Crow	AMCR	**Grasshopper Sparrow**	**GRSP**
American Goldfinch	AMGO	Great Crested Flycatcher	GCFL
American Robin	AMRO	House Sparrow	HOSP
Baltimore Oriole	BAOR	Indigo Bunting	INBU
Barn Swallow	BARS	**Killdeer**	**KILL**
Bell's Vireo	BEVI	**Lark Sparrow**	**LASP**
Blue Grosbeak	BLGR	**Mourning Dove**	**MODO**
Blue Jay	BLJA	**Northern Bobwhite**	**NOBO**
Brown Thrasher	BRTH	Northern Cardinal	NOCA
Brown-headed Cowbird	**BHCO**	Northern Mockingbird	NOMO
Carolina Wren	CARW	Orchard Oriole	OROR
Common Grackle	COGR	Red-bellied Woodpecker	RBWO
Common Nighthawk	**CONI**	**Red-winged Blackbird**	**RWBL**
Dickcissel	**DICK**	**Scissor-tailed Flycatcher**	**STFL**
Eastern Bluebird	**EABL**	Tufted Titmouse	TUTI
Eastern Kingbird	**EAKI**	**Upland Sandpiper**	**UPSA**
Eastern Meadowlark	**EAME**	**Western Meadowlark**	**WEME**
Eastern Phoebe	EAPH	Wild Turkey	WITU
European Starling	EUST	Yellow-billed Cuckoo	YBCU
Field Sparrow	**FISP**		

* American Ornithological Union 4-letter Alpha Code (Pyle & DeSante, 2014)

Disturbance

Burn status was derived from the 2000-2010 fire history maps created by Rhett Mohler (2011). Mohler mapped spring burning in the Flint Hills of Kansas and Oklahoma using satellite imagery (TM and MODIS) and in situ spectrometry, identifying the area of grassland burned each year, as well as the cumulative number of burns (0-11) over the study period. The majority of prescribed burns occurred in April, but the proportion of total area burned varied between years, ranging from a high of 48% in 2005 to a low of 15% in 2007 (Mohler & Goodin, 2012). Eighty-one percent of all grasslands in the study area were burned at least once over the study

period, but only 1% were burned annually. For each year, the area burned was first intersected with all grasslands (core habitat) before calculating the percentage of grassland area burned within 400m of each BBS stop location, a buffer size chosen as consistent with BBS protocol as the limit of visual and audible detection of a species by a stationary individual (Robbins, et al., 1986). All geoprocessing operations were performed in ArcGIS, version 10 (ESRI, 2011). The percentage of area burned within each stop buffer ranged from less than 1% to 100%. In an effort to compare equivalent habitats, only stops where core habitat accounted for at least 50% of the buffered area were considered. Of these, stops where less than 5% of the buffered area was burned were classified as *NoBurn*. Stops where at least 50% of the buffered area was burned were classified as *Burn.* Stops where the burned area was greater than 5%, but less than 50%, were omitted from further analysis. To balance sampling effort between groups, an equal number of stops representing each burn status were randomly selected from the total available for each year. Because the number of acceptable sites burned in 2006 and 2007 was exceptionally low (18 and 4, respectively), those model years were combined. The total number of acceptable stops over all years was 690, with the number in each study year ranging from a low of 40 in 2002 and 2006/2007, to a high of 120 in 2009. The area burned within *Burn* site buffers ranged from 69.06 to 77.60%.

Diversity and Similarity

To characterize assemblage structure, *Burn* and *NoBurn* stops in each study year were compared based on indices of diversity and compositional similarity that are commonly used in ecological research and are appropriate for explanatory studies based on bird survey data (Johnson, 2008). Diversity was explored using the complete list of species, hereafter referred to

as *all species*, or using only *grassland* species or only *shrub-woodland* species (see Table 2). All diversity indices and similarity measures were computed in R (R Core Development Team, 2006) using package *vegan*, version 2.4-2 (Oksanen, et al., 2017), *dismo*, version 1.1-1 (Hijmans, et al., 2016), and *gbm*, version 2.1-1 (Ridgeway, 2015), supplemented by R packages *BiodiversityR* (Kindt & Coe, 2005), *epi*, version 3.3.2 (Carstensen, et al., 2016), *dunn.test* (Dinno, 2017), *goeveg* (Friedemann & Schellenberg, 2017), and *sm* (Bowman & Azzalini, 2014). Statistical significance, where considered, was evaluated at the 95% confidences level (α=0.05). All tests requiring permutation were set at the default of 999. Alpha levels for all multiple comparisons were adjusted post hoc using Dunn's Test for multiple comparisons, with a Bonferroni correction method (function "dunn.test" in R package *dunn.test*).

In addition to species richness (S, or Hill number 0, H_0) and relative and rank abundance (N), diversity was assessed using two measures: Shannon entropy (*H'*) and Simpson concentration *(D_S)*, both converted to effective number of species form (Hill numbers) (Jost, 2006). Shannon entropy weights species by their relative abundance, so it is sensitive to changes in the number of rare species, whereas Simpson concentration represents the probability that two individuals selected at random will be the same species, so it is less sensitive to changes in species richness (S) than *H*' (Magurran 2004; Maurer and McGill, 2011). The formula for Shannon entropy is $H' = -\Sigma p_i \ln p_i$, where p_i is the proportion of the *i*th species; taking the exponent of *H'* is Hill number 1 (H_1) (Jost, 2006). Simpson concentration is calculated as $D_S = \Sigma pi\text{^}2$, where pi = ni/N and n_i is the number of individuals in a particular species; taking the inverse of D_S is Hill number 2 (H_2) (Jost, 2006). Evenness was calculated as H_1 / H_0. Difference in species richness and relative abundance between burn groups was also explored using kernel density estimation plots, sample-based species accumulation curves, and rank

abundance plots. Diversity indices between burn groups were compared directly by calculating a ratio of the mean value of each index for the *Burn* group divided by the mean value of that index for the *NoBurn* group, and assessing the magnitude of the difference (calculated as 1 – ratio value).

Annual *Burn and NoBurn* stops were also compared based on ecological distance (community dissimilarity) using pairwise distance matrices of Euclidean distance between stops versus the binary Jaccard Similarity Index, which reflects the overlap of species between observations (number of shared species/the total number of species in both plots) (Jost, et al., 2011). Similarity based on occurrence emphasizes rare species, because most species in a community are rare and presence/absence data weights them all equally; in contrast, abundance-based similarity is influenced most by common species (Dornelas, et al., 2011; Magurran & Henderson, 2011). Two communities sharing the same species in the same relative abundances have high similarity. An analysis of similarities (ANOSIM, Clarke, 1993) was used to visually examine community composition between and within burn groups based on Jaccard similarity (function "anosim" in R package *vegan*). In addition, a version of nonparametric multivariate analysis of variance (NPMANOVA, Anderson, 2001) was used to judge the statistical significance of any difference in assemblage structure between and within *Burn and NoBurn* stops (function "adonis2" in R package *vegan*). Mantel tests were used on Jaccard and Euclidean distance matrices to evaluate the possible confounding effects of geographic location on community similarity.

Assemblage similarity was also explored through nonmetric multidimensional scaling (NMDS, Clarke, 1993) which is a rank-based, unconstrained ordination technique that illustrates underlying patterns in community structure based on ranked dissimilarities between pairs of

samples. NMDS ordination (function "metaMDS" in R package *vegan*) was used to plot sites in "ecological space" based on Jaccard and Euclidean distance matrices. The distance between points in ordination space approximates the rank order of the original dissimilarity values; therefore, communities that are more similar in composition are plotted as nearby points, whereas those more dissimilar are further apart. NMDS ordination generates stress values that measure the disagreement between the rank order of similarity values in the original data and that in ordination space; lower numbers indicate better agreement. Stress values approaching 0.3 indicates that ordination is arbitrary, above 0.2 is suspect, 0.1 is fair, and a value at or below 0.05 indicates good fit (McGarigal, et al., 2000). To reduce stress values, the NMDS algorithm was first run using a random initial placement of objects and a high number of dimensions (10). The point coordinates and distances from the best solution in the high-dimension NMDS run were extracted and used as the approximate starting point for a subsequent NMDS run using a lower dimension (3). Both ordinations were run with the same minimum ('try'=100) and maximum ('trymax'=500) number of starts in search of a convergent solution. The lower-dimension NMDS was plotted, with labels for the most abundant species (top 30%) and standard deviation ellipses of group centroids according to burn status (functions "ordiselect" and "ordiellipse" in R package *BiodiversityR*).

III. Results

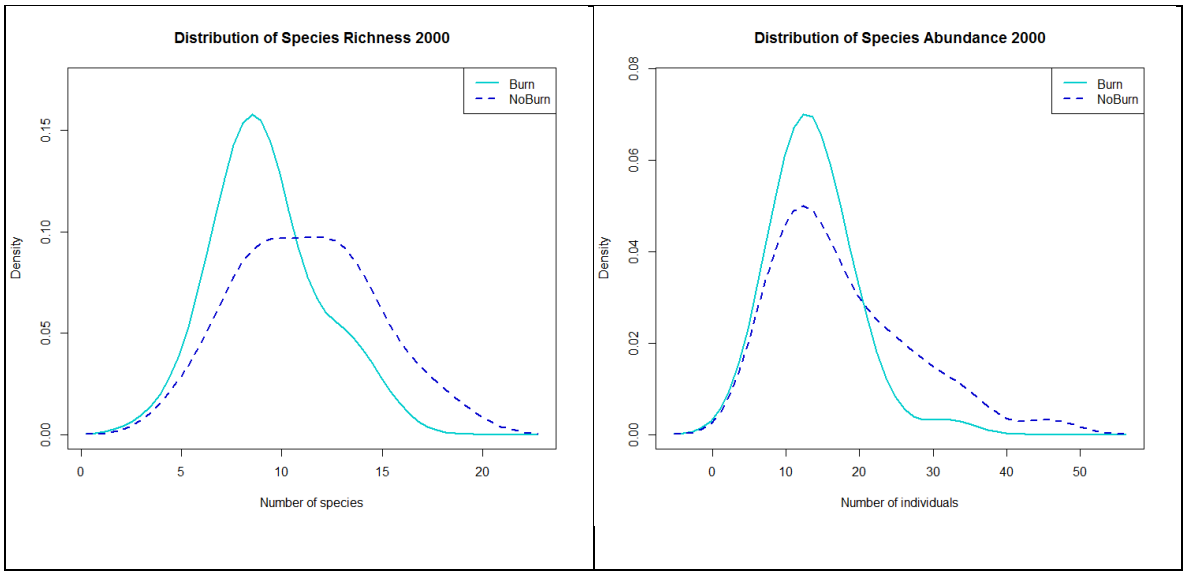
Differences in stop species richness and relative abundance between *Burn and NoBurn* sites was evaluated using Mann-Whitney U tests and displayed using kernel density estimation (KDE) plots and species accumulation curves. For study years 2004, 2005, 2008, and 2010, there were no statistically significant differences in species richness or relative abundance

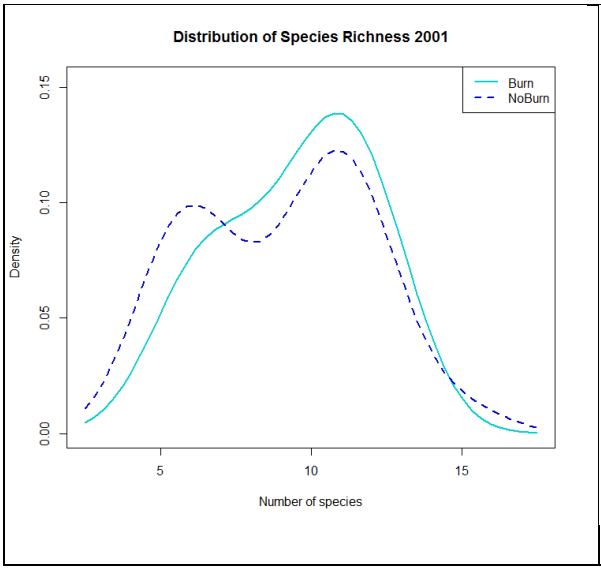
between burn groups for *all species* combined, or for *grassland* or *shrub-woodland* species groups considered separately. In 2001 and 2009, there was no statistically significant difference in species richness between *Burn and NoBurn* stops for any species group. Species richness was statistically significantly different for *all species* as a group in 2000 (p=0.012), in 2002 (p=0.009) and in 2006/2007 (p=0.008). Species richness was statistically significantly different for *grassland* species in 2006/2007 (p=0.001) and for *shrub-woodland* species in 2000 (p=0.0003) and 2003 (p=0.029). Relative abundance was statistically significantly different for *all species* in 2006/2007 (p=0.0002) and 2009 (p=0.015); for the *grassland* species group in 2001 (p=0.034) and 2006/2007 (p=0.019); and for the *shrub-woodland* species group in 2000 (p=0.0014), 2003 (p=0.02), and in 2006/2007 (p=0.0003).

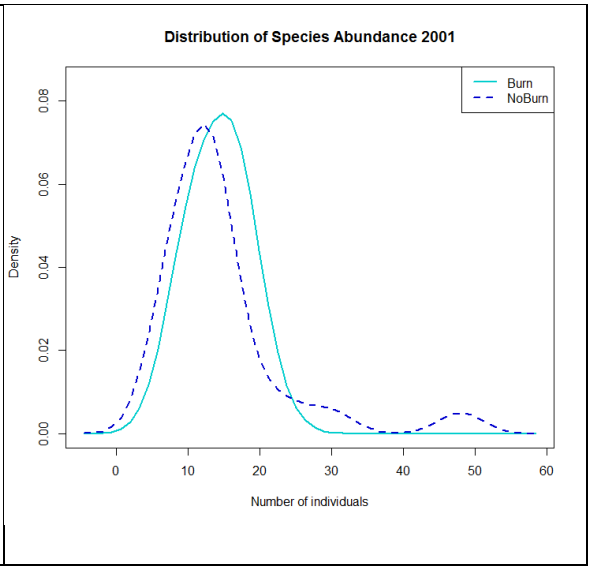
Similar outcomes were found by plotting the results of kernel density estimation (function "sm.density.compare", in R package *sm*). Significance is calculated within the R function and is based on a permutation test for equality. Kernel density estimation (KDE) is a non-parametric method to model the distribution of a population based on a finite data set. In Using KDE, the probability density function for species richness and abundance in each year was calculated for *Burn* and *NoBurn* groups. Curves for each burn group were plotted on a single graph and compare and differences between groups were evaluated based on a permutation test of equality. For the study years, 2003, 2004, and 2008, there were no statistically significant differences ($p<0.05$) in the density distribution of species richness or relative abundance between *Burn and NoBurn* stops for *all species* combined, or for *grassland* or *shrub-woodland* species groups considered separately. For *all species*, there was a statistically significant difference in species richness between *Burn and NoBurn* sites in 2000 (p=0.02), 2002 (p=0.009), and 2006/2007 (p=0.01) and for relative abundance in 2000 (p=0.05), 2001 (p=0.04), 2006/2007

(p=0), and 2009 (p=0). For the *grassland* group, there was a statistically significant difference in species richness between *Burn and NoBurn* sites in 2002 (p=0.05) and for relative species abundance in 2000 (p=0.05) and 2006/2007 (p=0). Based on KDE, species richness was only statistically significantly different for the *shrub-woodland* group in 2010 (p=0.04); there was no statistically significant difference in relative abundance between *Burn and NoBurn* stops in any study year. Selected KDE plots showing the density distribution of richness and abundance for the *all species* in study years are presented in Figure 1.

FIGURE 1: Kernel density estimation (KDE) plots of species richness and abundance between *Burn* and *NoBurn* sites for the *all species* group. In each plot, KDE curves are show in a solid cyan line for *Burn* sites and a dashed blue line for *NoBurn* sites. KDE plots shown are those for which there was a statistically significant difference in the probability density function between burn groups for either specie richness or abundance. Both species richness and abundance were statistically significant different in study years 2000 and 2006/2007. Statistically significant differences between burn groups for abundance only occurred in 2001 and 2009, and for species richness only in 2002.




Distribution of Species Richness 2001
Burn
NoBurn
Density
0.00
0.05
0.10
0.15
5
10
15
Number of species


Distribution of Species Abundance 2001
Burn
NoBurn
Density
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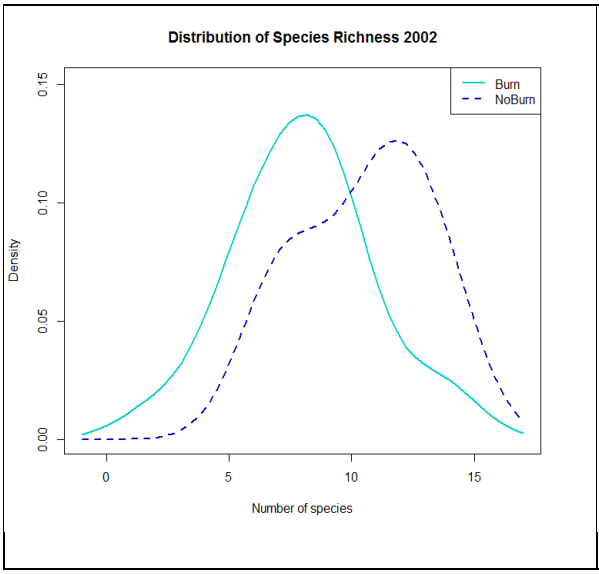
0.02
0.04
0.06
0.08
0
10
20
30
40
50
60
Number of individuals


Distribution of Species Richness 2002
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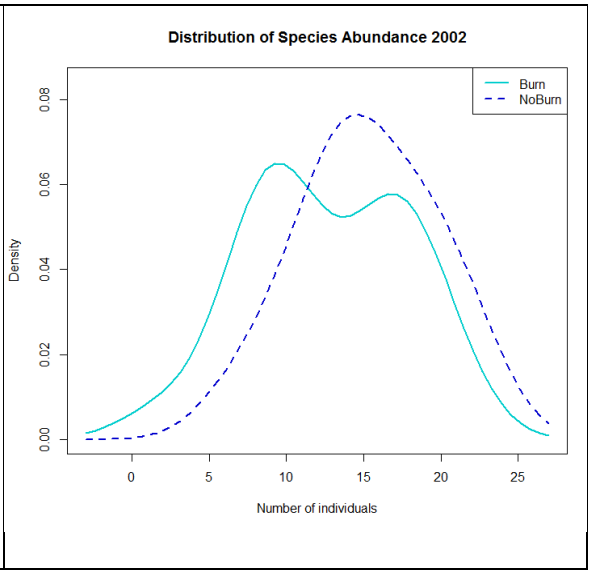
NoBurn
Density
0.00
0.05
0.10
0.15
0
5
10
15
Number of species


Distribution of Species Abundance 2002
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NoBurn
Density
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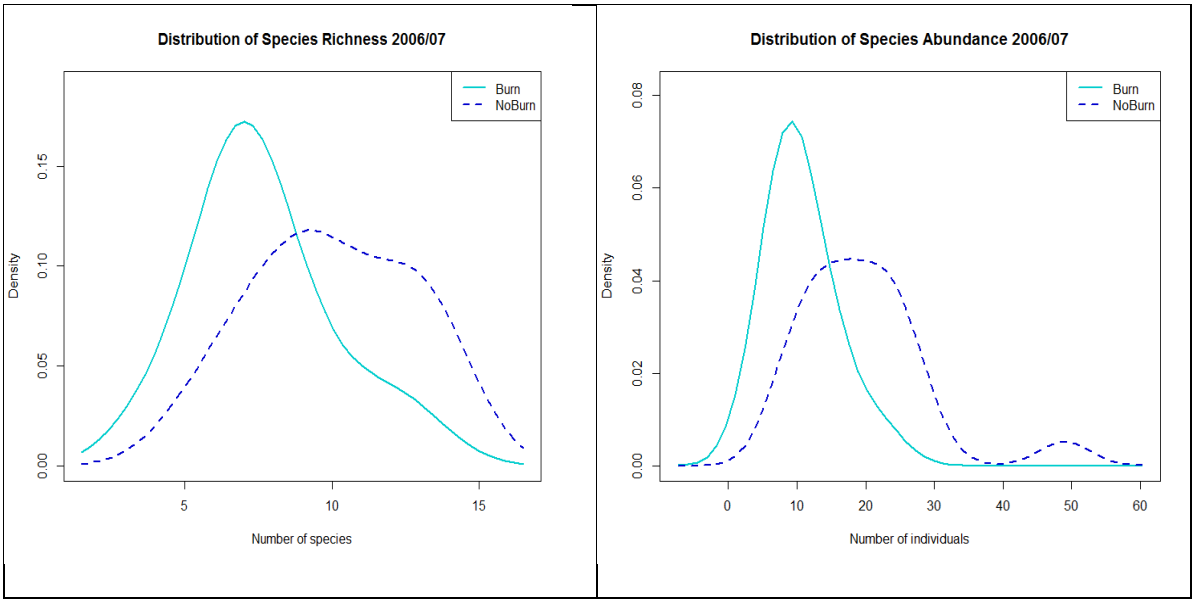
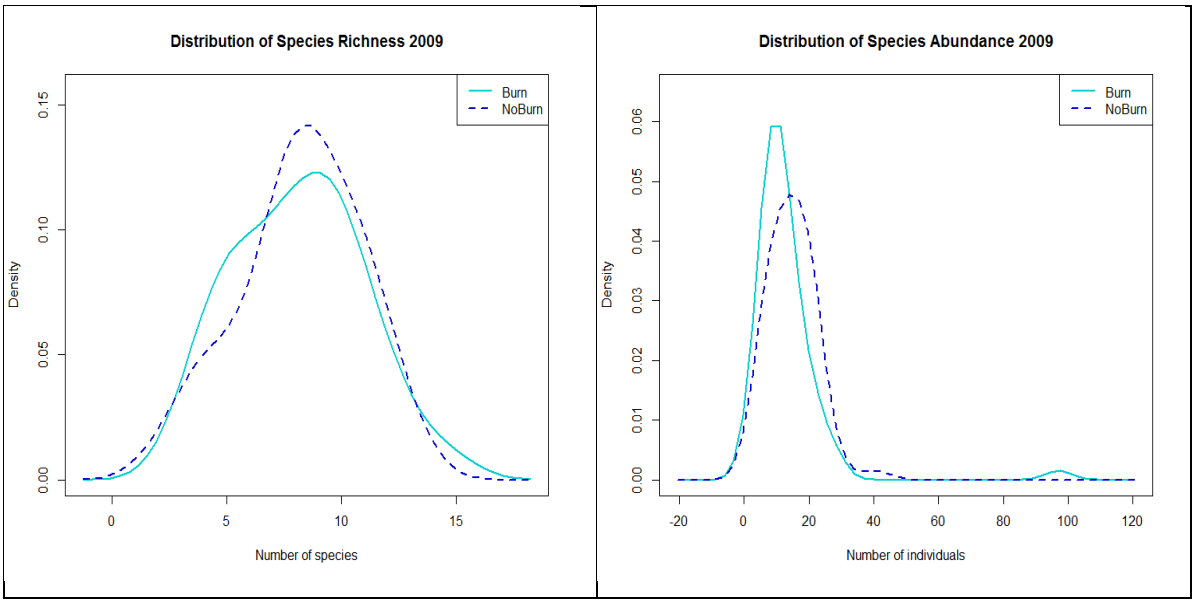
0.04
0.06
0.08
0
5
10
15
20
25
Number of individuals





Species were also ranked by relative abundance at each stop and *Burn and NoBurn* stops compared based on Spearman rank order correlation. There was a statistically significant difference in rank abundance order between *Burn and NoBurn* stops for the *all species* group (p=0.003) in 2008, but for no other group in any other study year. Species richness between burn groups was compared using sample-based species rarefaction curves. Sample-based

rarefaction is a method of correcting for bias in estimates of species richness that result from unequal sampling effort. Curves show the mean number of species expected based on the number of samples collected. Rarefactions curves were plotted separately for each burn group and plotted on the same graph for comparison. A separation between curves by burn groups was seen in 2000 and somewhat in 2009 and 2010, indicating species richness differences between burn groups, but there was minimal separation between curves for other years. Species rarefaction curves for *all species* are shown in Appendix 7.

A summary of all diversity indices over all study years is listed in Appendix 8. When examining diversity index ratios between *Burn* and *NoBurn* sites, the magnitude of any difference less than 5% was ignored. Based on diversity index ratios for *all species*, *Burn* sites had lower diversity than *NoBurn* sites in terms of mean species richness in four of ten study years, and for Shannon entropy and Simpson's concentration in three of ten study years. The difference was greatest for the *shrub-woodland* species group, where the three indices of diversity were lower by an average of 32% at *Burn* stops in at least eight of ten study years. In contrast, species richness and the Shannon and Simpson indices for the *grassland* species group were higher at *Burn* stops in at least five of the ten study years. Evenness did not differ between *Burn and NoBurn* sites with four exceptions: for all of the species groups in 2006/2007 and for the *shrub-woodland* species group only in 2002, where burned sites had greater evenness.

Community composition based on the Jaccard similarity was evaluated based on NPMANOVA results, ANOSIM plots and through NMDS ordination. Based on the results of Mantel tests for all species groups in each year, assemblage similarity was statistically significantly correlated with geographic distance between stops (p=0.001). Based on NPMANOVA results, differences in assemblage structure between *Burn and NoBurn* sites were

statistically significant ($p<0.05$) for the *all species* group in all years except 2004, 2008, and 2010. For the *grassland* species group, differences in assemblage structure according to burn status were statistically significant ($p<0.05$) in all years except 2003, 2004, 2008, and 2010. For *shrub-woodland* species, community composition was statistically significantly different ($p<0.01$) for *Burn and NoBurn* sites for all years except 2001, 2004, 2005, 2006/2007, 2008, 2010. ANOSIM boxplots showing mean similarities within and between burn groups are presented in Appendix 9.

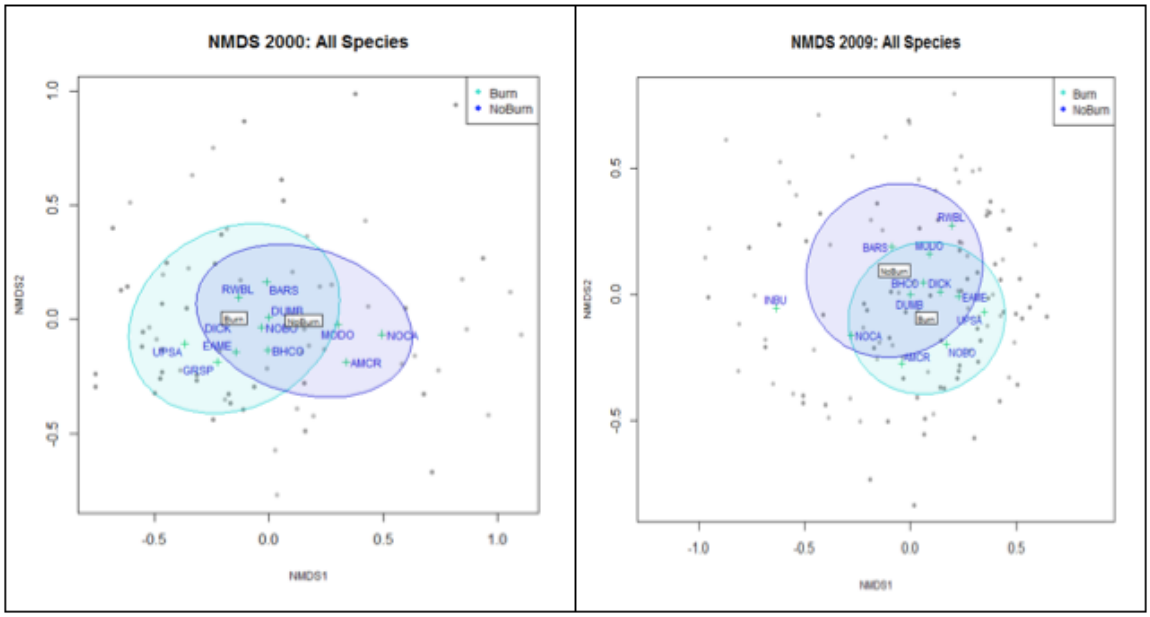
NMDS plots for the all species groups are shown in Appendix 10. Stress values generated by the ordination process indicate how faithfully the original dissimilarity values are represented in the reduced ordination space; lower stress values are better than higher ones. When distance matrices for the *all species* group were considered, the stress values ranged from a low (best) value of 0.17055 in 2000 to a high of 0.20379 in 2009, with an average value of 0.1839. NMDS ordinations with a value above 0.2 are of limited value (McGarigal, et al., 2000). A second year for the *all species* group, in 2008, also had an ordination stress value greater than 0.2. For the *grassland* species group, stress values ranged from a low (best) of 0.12837 in 2006/2007 to a high of 0.17667 in 2010; the average stress value for this group was 0.1492. Stress values for the *shrub-woodland* group were in the middle, ranging from a low (best) of 0.13628 in 2010 and a high of 0.18401 in 2003, with an average ordination stress value of 0.1640. The best and worst NMDS plots for each species group are shown in Figure 2. It is interesting to note that 2010 had the highest stress score for the grassland species group, but the lowest stress score for the shrub-woodland group.

FIGURE 2: Nonmetric multidimensional scaling (NMDS) ordination plots based on the binary Jaccard Index of community similarity between *Burn* and *NoBurn* sites. Standard deviation ellipses are drawn around *Burn* (cyan) and *NoBurn* (blue) group centroids. Small gray circles represent site locations; slightly darker gray circles are *Burn* stops. Sites plotted closer together in ordination space have more similar avian communities. Green crosses represent the top 30% most abundant species, labeled using AOU Codes (see Table 2); "DUMB" identifies the dummy species added to each data set.

Best (left) and worst (right) NMDS plots for *all species* (A), *grassland* species (B), and *shrub-woodland* species (C). Stress values measure the disagreement in the rank order of Jaccard Index values in the original data and that in ordination space; lower numbers indicate better agreement.

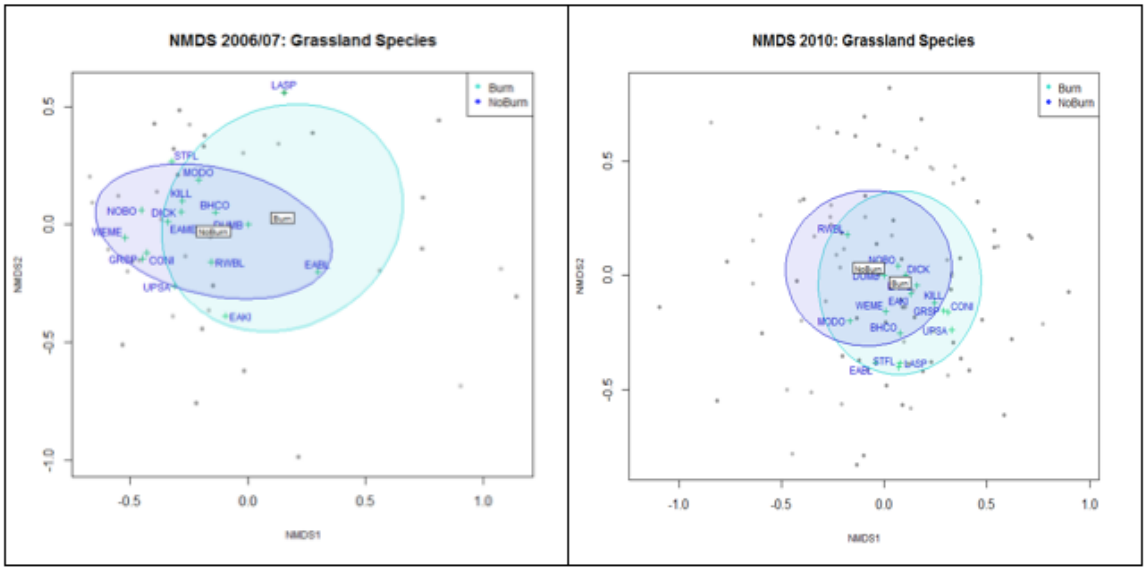
A. NMDS, all species

Stress=0.17055 Stress=0.20379



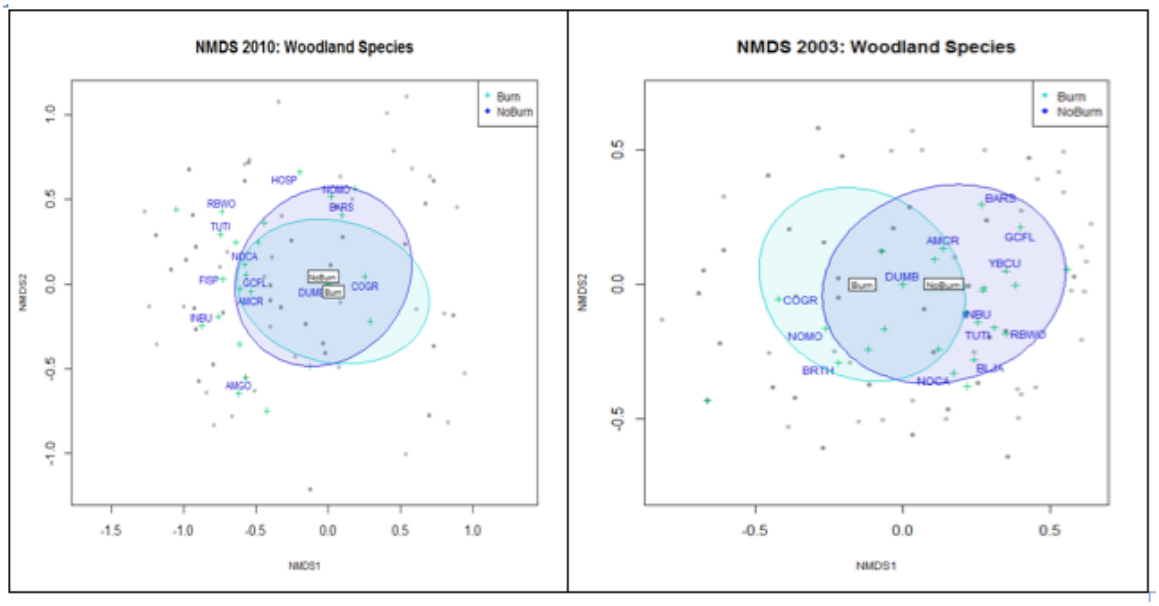
B. NMDS, grassland species

Stress=0.12837 Stress=0.17667



C. NMDS, shrub-woodland species

Stress=0.13628 Stress=0.18401



IV. Discussion

Although not definitive across all years, diversity as measured by standard indices for species richness, Shannon entropy, and Simpson's concentration was lower at *Burn* sites than at *NoBurn* sites at least a third of the time for the *all species* group and at least 80% of the time for the *shrub-woodland* species group. Not surprisingly, the *grassland* species group showed an opposite result, with *Burn* sites showing higher diversity more than half of the time. The metric for evenness was rarely different between *Burn and NoBurn* sites; where it was, burned sites had greater evenness (i.e. were more diverse) than unburned sites. This situation occurred for all of the species groups in the 2006/2007 and for *shrub-woodland* species group only in 2002.

The greatest difference in magnitude between *Burn and NoBurn* sites for all diversity indices ratios seemed to be concentrated in certain years, and thus may be related to specific conditions occurring in those years rather than reflecting a predictable response to disturbance by burning. Specifically, for the *all species* group, the difference in diversity measured by species richness and Shannon and Simpson indices was greatest in study years 2000, 2002, and 2006/2007. For the *grassland* species group, differences in species richness were greatest in 2001, 2002, and 2006/2007; for the Shannon and Simpson indices, the differences were greatest in 2001, 2002, and 2009. With the *shrub-woodland* species group, differences in these diversity indices were greatest in 2000, 2001, and 2006/2007. Model year 2006/2007 was important for all groups in terms of diversity differences between burn groups; this study year tied with 2002 for the fewest number of observations, and had the lowest average percentage burned within *Burn* sites, as well as the lowest total percentage burned of all study years. Because this model year represented two burn seasons in which minimal acreage was burned, it seems reasonable to expect that some of the *NoBurn* sites in model year 2008 had several consecutive years without

burning and so had more woody vegetation than would be expected with more frequent burns. This may be why 2008 was the only model year where there was a statistically significant difference between *Burn and NoBurn* sites in terms of rank abundance.

The importance of particular years as reflected in metrics for species richness and relative abundance is reaffirmed by the results from kernel density estimation (KDE); KDE plots showed statistically significant differences in species richness between *Burn and NoBurn* sites for study years 2000-2002 and again in the 2006/2007 model year for the *all species* group, and in 2002, 2006/2007, and 2009 for the *grassland* species group. KDE plots for abundance showed statistically significant differences between *Burn and NoBurn* sites for study years 2000, 2001, 2006/2007, and 2009 for the *all species* group, and in 2002, 2005, 2006/2007, and 2009 for the *grassland* species group. For the *shrub-woodland* group, only model year 2010 had a statistically significant difference in species richness between *Burn and NoBurn* sites as calculated by KDE; no model years showed a statistically significant difference in abundance for this group.

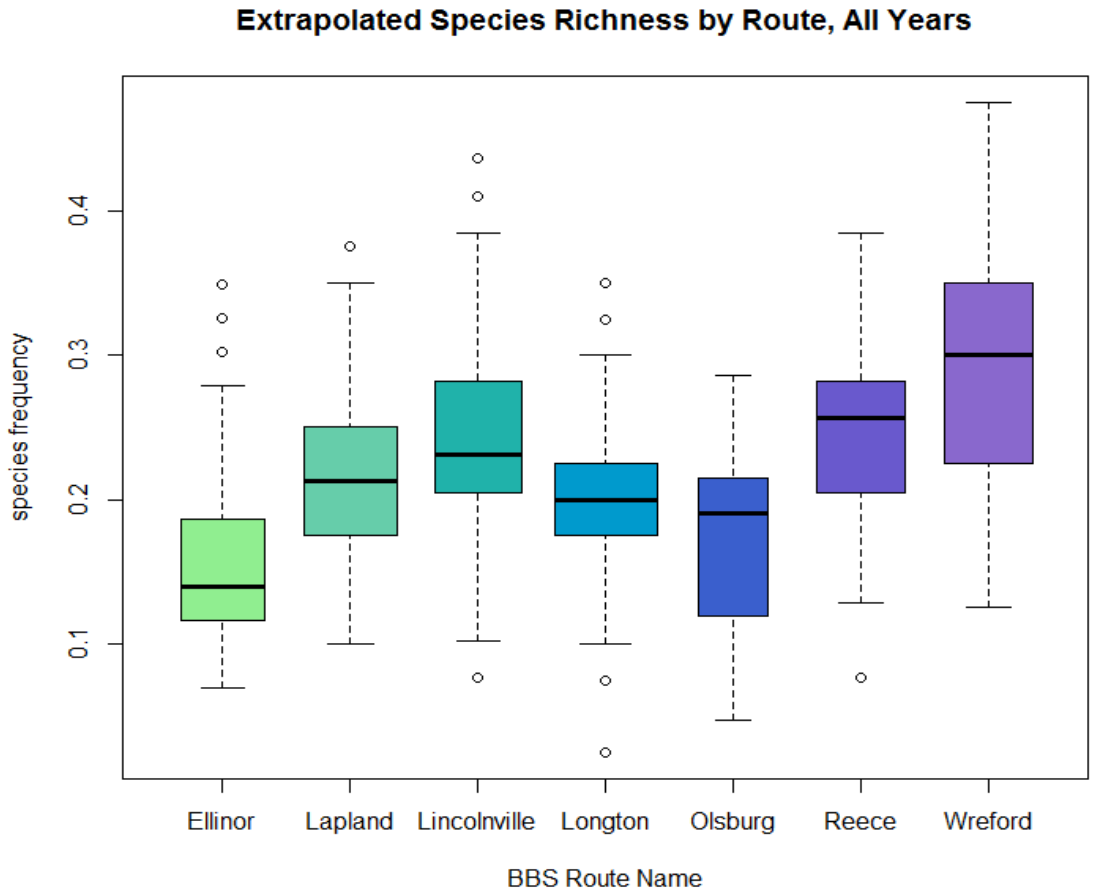
The apparent trend for some years being more influential in determining diversity continued upon examination of differences in assemblage structure. When data from *Burn and NoBurn* sites were examined using NPMANOVA, between-group similarity was statistically significantly greater than within-group similarity in most cases for all study years except for 2004, 2008, and 2010. The ability of NMDS to represent original dissimilarities in reduced ordination space was mediocre at best when *all species* were used, but marginally better when the subgroups with more specific habitat needs were considered separately. It is possible that initially placing objects in ordination space based on Euclidean distance or principal component analysis might have improved results (Legendre & Legendre, 2012). The NMDS ordinations

with the least stress in each group again overlapped particular years. For instance, the two study years with the lowest ordination stress values were in 2000 and 2002 for the *all species* group, in 2002 and 2006/2007 for the *grassland* species group, and in 2005 and 2010 for the *shrub-woodland* species group. It is unclear why certain years had more impact on diversity and community structure between *Burn* and *NoBurn* sites, but it seems reasonable to suspect that some combination of weather conditions influenced vegetation structure, or perhaps impacted the severity or extent of burning in those years. Since most of the included species are migrant, these years might also by chance have coincided with some unknown factor affecting wintering survival or migration times.

Finally, that community composition would be correlated with distance is not surprising since Kruskal-Wallis nonparametric analysis of variance tests showed that extrapolated species richness was statistically significantly different between routes in each single year, as well as when species data for all years were combined, as shown in Figure 3. This difference is likely because available habitat for grassland birds varies across the study areas, but could in part relate to the skill of route observers. The difference in species richness between routes in turn impacted diversity indices for combined years, resulting in statistically significant differences in diversity indices between routes for the *all species* group. Species richness, Shannon entropy, Simpson's concentration, and the Evenness Index were also statistically significantly different between routes for both the *grassland* and *shrub-woodland* groups. Total relative abundance for the *all species* group was not different between routes; however, the total relative abundance for both the *grassland* and *shrub-woodland* groups were statistically significantly different between routes. Ideally, annual stops would have been stratified by route; however, there were too few acceptable stops in most years to make any further division of stops practicable. Similarly,

extending this study to an investigation of the cumulative effect of burning over the study period was planned, but unfeasible because of the extremely small sample size for each aggregate burn category. The wide-ranging percentage of area burned across all stops within each aggregate burn year would also have made analysis unrealistic.

FIGURE 3: Box-and-whisker plot showing extrapolated species richness by route across all years.



There are many factors that could determine differential habitat selection by grassland birds. For instance, habitat use could be impacted by the size of the available habitat, including the influence of perimeter to habitat edge, spatial patchiness, and the isolation of the particular

patch. Biotic factors may also influence habitat selection, such as the structure of the habitat and the number of the available niches or microhabitats. Competition and predation, dispersal limitations, foraging behavior, territoriality, and philopatry may also impact habitat use. In addition, some species may naturally have a high degree of variation between years and others might be impacted by conditions at wintering grounds that have little to do with counts in the breeding season. Habitat use is also a matter of perception, highly dependent on the method by which organisms are counted. In this project, abundance was determined based on a single count; species may use the specific habitat, but not be discovered or may not yet be present. Migrant species included in this study have different arrival times, reach peak abundance at different times, and have different nesting modes that might not coincide with the route census in a particular year.

In the Flint Hills, the main types of regular, repeated disturbance are grazing, mowing and burning. The impact of disturbance depends in part on the type of disturbance and whether it is severe, but occasional, or low-level and frequent. Interpretation of the impact of spring burning in this study was complicated by a number of factors. First, this study considered burning as the disturbance, but did not factor in disturbances that could come from the type and intensity of range use after burning. Sample sizes for each burn category were equal within a year, but not equal between years, and although the sites were divided into two 'treatments', *Burn* or *NoBurn*, they were not truly dichotomous categories. Although no burning occurred in the spring of the model year for the *NoBurn* stops, these sites could have been burned in the fall or winter prior to the breeding season. Also, these *NoBurn* sites represent many successional stages, since no attempt in this study was made to identify when they were last burned, if ever.

These caveats apply to *Burn* sites as well, but that category has additional issues. First, the burned data used in this study varied in accuracy between years (Mohler, 2011). *Burn* sites in all years represent burning that ranges in extent from 50-100%; however, since the initial requirement was that all sites considered had to have *at least* 50% of the buffered area in 'core habitat', this means that sites where burned grasslands represented 25% of the buffered area were considered equivalent to sites where burned grasslands comprised 100% of the buffered area. For both categories, only sites that had at least 50% 'core habitat' within the buffered area were included in the study; however, the core habitat designation is comprised of both cool season and warm season grasslands, which might attract different species. Likewise, the requirement for 50% grasslands did not specify a minimum patch size or a specific perimeter-area ratio, both factors that can limit habitat use by area-sensitive birds such as the Upland Sandpiper. For most sites in both categories, core habitat made up less than 100% of available landcover; however, other landcover types within those buffers, which could have impacted habitat use, were not identified. Similarly, the amount of available habitat in the surrounding landscape was also not considered.

CHAPTER 4: CONCLUSION

Abstract

Temperate grasslands are among the most vulnerable, least protected biomes on earth. In North America, tallgrass prairies are particularly endangered, having lost between 82-99.9% of their original extent since the advent of European settlement. Most tallgrass prairie acreage was lost outright to agriculture and development. Much of the remainder persists as small, isolated grasslands or is degraded through intensive management and the alteration of historic fire regimes. Given the drastic loss, fragmentation, and alteration of grassland habitat, a consequent decrease in the abundance of grassland birds is not unexpected. An overall downward trend in grassland bird numbers has been noted since avian population monitoring began in North America in the 1960s, prompting various conservation groups to include the affected species on national watch lists, as priority species, or as species of conservation concern. Because of their declining populations, identifying the environmental and landuse factors that influence habitat selection by grassland birds has become a critical tool for effective conservation management.

Species Modeling

Boosted regression tree (BRT) models were constructed for fifteen avian species know to inhabit the Flint Hills region of Kansas, using annual count data obtained from the Breeding Bird Survey (BBS). Focal species varied in their dependence on grassland habitat and in their specific habitat preferences, including their tolerance of or reliance on woody vegetation. Species also varied in their functional traits, migratory pattern, and expected response to burning. Models included explanatory variables describing landscape, climate, and disturbance, as well as BBS

route information. BRT models were calibrated separately, using metaparameters that optimized model fit and predictive performance for each individual species. In addition to evaluating model success based on fit and performance, the relative importance of predictors was examined. Partial dependence plots showing the marginal effect of a single variable on the response were also analyzed. Species models were reviewed individually and grouped with other species sharing similar habitat requirements.

In general, model fit and performance was better for species with greater abundance and prevalence. Species with relatively narrow habitat requirements, such as the Upland Sandpiper, also had models with better fit and performance compared to those for species with more general habitat preferences, like the Mourning Dove. On average, models for shrub-woodland species had the lowest misclassification error, as measured by mean estimated cross-validation holdout residual deviance (CV deviance). For obligate grassland species, which rely on grasslands for all or part of their life cycle, average CV deviance was higher than for facultative grassland species, which commonly use grasslands, but are not restricted to that habitat. Even within the facultative grassland species group, the model for the species with the most narrow habitat preferences, the Common Nighthawk, had the lowest misclassification error.

The availability of preferred habitat combined with prevalence also seemed to impact model success. For example, the most successful model based on CV deviance was the Red-headed Woodpecker. This species has more restricted habitat preferences than some others in the shrub-woodland group, preferring more mature, open woodland with a grassy rather than shrubby understory. Although this species was the least abundant and prevalent species modeled, its more stringent habitat requirements coupled with a relative paucity of preferred habitat across the study area may have reduced the misclassification error for this species. In

contrast, the worst model performance based on CV deviance was for the Mourning Dove, a widespread and abundant species. Although classified by Vickery, et al (1999) as a facultative grassland species, the Mourning Dove is considered by some to be a habitat generalist (Poole, 2005) because of its use of a broad range of open and semi-open habitats including forest clearings, farmland, prairies, suburbs, and deserts. The BRT model for the Mourning Dove was likely less successful because the general habitat requirements for this species made it harder for the model algorithm to ascribe species occurrence to a specific habitat type.

The connection between species abundance and habitat specificity and model fit and performance was confirmed when models were evaluated based on the area under the Receiver Operating Characteristic (ROC) curve, a metric used for judging the diagnostic ability of a binary classifier. The model with the highest ROC score was for the Western Meadowlark, an obligate grassland species found in more xeric prairies with shorter grasses and less litter. This species was not abundant (total abundance of 391) compared to some other species modeled, but was present on only three routes (26 annual surveys); therefore, the dataset for this species was not as sparse as some others. However, because species occurrence was restricted to only three routes, the ratio of predictors to observations was higher than for other species, which may have contributed to this model's occasional "failure to converge". The least successful model based on ROC score was for the Bell's Vireo. This species had a total abundance (169) that was less than half that of the Western Meadowlark, but it was present on all seven routes (59 annual surveys), yielding a relatively sparse data set. Average ROC scores were highest for the obligate grassland group and lowest for the shrub-woodland group. For the facultative grassland group, the model for the species with the most narrow habitat preferences (Common Nighthawk), again had the best model fit and performance; the model for the species with the broadest habitat

requirements (Mourning Dove), had the worst model performance. BRT model results were also evaluated based on the percent deviance explained by the fitted model. Again, model performance was highest for the Western Meadowlark and lowest for the Mourning Dove. When considered as a group, obligate grassland species models on average explained 60% of the model deviance, whereas the facultative grassland and shrub-woodland species groups explained only 43% and 42%, respectively. In comparison, the least successful model in the obligate grassland group, for the Grasshopper Sparrow, explained 47% of model deviance.

Model misspecification may be another factor in determining differences in model performance between species. All models were constructed using the same set of 65 explanatory variables, and then simplified to a set of 30 variables unique to each species. For the simplified models, the top fifteen predictors accounted for an average of at least 75% of the total relative variable influence. The most influential single variable was *RTEsection,* a predictor derived by dividing each route into ten consecutive sections beginning from the route starting point and assigning each stop a number based on the route section in which it occurred. This variable was intended as a surrogate for time since dawn, but may have inadvertently captured the effects of terrain and associated woody vegetation instead. For example, the partial dependence plot charting the marginal effect of this variable on the response (species occurrence) in the model for the Common Nighthawk, showed that the earliest route section had a high positive impact on the response, as would be expected for this crepuscular species. However, partial dependence plots for this variable in other species models showed a scattered or fluctuating pattern of impact on occurrence, suggesting that this variable was not capturing what was intended. Another route variable, identifying the route *Observer,* may also have represented available habitat, rather than the impact of different observers as intended. Whether denoting model misspecification or not,

these two variables together likely accounted for the dominance of 'route' variables in the top five most influential variables across all species models.

In the simplified models, landcover predictors were the most influential suite of variables for obligate grassland and shrub-woodland groups. These groups differ in their response to woody vegetation, but within each group the habitat requirements for each species is relatively narrow. In contrast, the facultative grassland species group contains species with relatively narrow habitat requirements, such as the Common Nighthawk and the Northern Bobwhite, as well as species with relatively broad habitat requirements, such as the Brown-headed Cowbird and the Mourning Dove. Vegetative structure and composition are well known as drivers of local bird abundance (MacArthur & MacArthur, 1961; MacArthur, et al., 1962; Wiens, 1973, 1974b; Rotenberry & Wiens, 1980; Cody, 1981; Zimmerman, 1992, 1997; Patterson & Best, 1996), so it is not surprising that landcover variables would be important in all species models. For facultative grassland species as a group, the suite of terrain variables had more total influence than landcover variables; however, this may in part also represent the influence of vegetation structure, since woody vegetation within the study area is often associated with certain terrain features, such as floodplains and ravines.

Grassland variables were generally more influential than woodland variables, but this could be because the grassland category was represented by six variables, including both broad and relatively narrow predictors, as compared to only two variables representing woody vegetation. Grassland patch variables were often more influential than simple proportional grassland cover, reflecting the importance of the patch size and perimeter to area ratio for a majority of the grassland species modeled. In addition, warm season grasslands had greater relative variable importance than cool season grasslands. This may represent the importance of

vegetation structure differences between the grass types, or it could reflect differences in land management for the two grassland types. All variables for burned grasslands were retained in simplified models, but the variable for area burned in the model year was retained in only four models. This variable was not retained in the model for the Common Nighthawk, as was expected based on its habit of laying its eggs on bare ground. Burning in the year prior to the model year was the most frequently retained burn variable, and had the greatest total relative variable influence.

Some climate variables were retained in all simplified models. In general, precipitation variables were more influential than temperature variables, likely reflecting the importance of precipitation on vegetative growth. However, the precipitation variable retained most often, the standard deviation of precipitation in summer, might be capturing the influence of extreme precipitation events on some grassland birds after the onset of nesting. Drought variables were present in all simplified models, but on the whole appeared less frequently and with smaller relative importance than other climate variables. All annual Palmer Drought Severity Index (PDSI) variables appeared in at least some of the simplified models, but only the six-month Standardized Precipitation Index (SPI) variables for April and May were retained. This could mean that drought conditions leading into the peak breeding season months of May and June are more critical than those prior to the peak month for burning (April) or after nesting has been initiated for most species.

Diversity and Disturbance

Differences in diversity and community composition between sites burned and those that remained unburned were investigated in the second part of this study. To ensure that relatively

equivalent habitats were compared, analysis was restricted to stops in which grassland habitat made up at least 50% of a 400m buffered area around each stop. For each year, eligible stops where less than 5% of the buffered area was burned were assigned to the *NoBurn* category. Eligible stops where at least 50% of the buffered area was burned were designated as *Burn* stops. Stops where 5-50% of the buffered area was burned were discarded. For each stop, common indices of diversity and the Jaccard Index of community similarity were calculated based on annual BBS count data. All years were considered separately except for study years 2006 and 2007; stops for these years were combined because of the low number of eligible *Burn* stops in each year.

In general, diversity as measured by species richness, Shannon entropy, and Simpson concentration was less in *Burn* sites than in *NoBurn* sites in three to four study years for all species combined, and in eight to nine study years for shrub-woodland species considered separately. For grassland species considered separately, *Burn* stops had greater diversity than *NoBurn* sites in five to seven study years. The loss of diversity in burned areas for all species combined and for shrub-woodland species considered separately likely reflects the temporary shift of shrub dependent species away from recently burned sites (Grant, et al., 2010). Diversity as measured by species evenness did not differ between *Burn* and *NoBurn* sites in any year except 2006/2007 for all the species groups, and in 2002 for the shrub-woodland group only.

For all groups in all study years, community similarity was statistically significantly correlated with geographic distance between stops. This result is not surprising since species richness differed between routes in individual years as well as when data for all years were combined; however, species abundance was not statistically significantly different between routes when data for all years and all species were combined. Based on nonparametric

multivariate analysis of variance (NPMANOVA), the difference in community similarity between *Burn* and *NoBurn* sites was statistically significantly greater between, rather than within burn groups for all species combined in all study years except 2004, 2008, and 2010. Although the ability to illuminate differences in community similarity between burn groups through nonmetric multidimensional scaling (NMDS) was only fair at best, the best results were in 2000 for all species combined, in 2006/2007 for grassland species only, and in 2010 for shrub-woodland species only.

Differences in diversity between stops grouped by burn status seemed to be concentrated in certain years. The reason for this apparent trend is unclear, but could be related to a combination of weather conditions that impacted vegetation structure or perhaps influenced the extent and severity of burning across the larger landscape. The intensity and duration of grazing pressure or timing and frequency of mowing may also have varied between stops and between years. Since most species present are migrants, differences in diversity, or lack thereof, might also have been impacted by conditions on wintering grounds that were unrelated to breeding habitat. Natural variation in individual species populations between years, including overwintering survival rates, could also explain diversity and community similarity differences between years.

Assumptions, Issues, and Improvements

For this project, 'disturbance' was defined simply as the removal of biomass through fire, but grazing and the interaction between fire and grazing also influence vegetation structure; not including these predictors likely impacted results. This study was based on the assumption that habitat heterogeneity increases diversity, but the concept of heterogeneity is scale dependent and

a mismatch between perceived and measured heterogeneity could have introduced bias. Because this study did not include a control/treatment element, there was an absence of baseline data prior to the study period and so avian responses described by this study are not independent of the influence of land management history. Neither are species responses necessarily independent of the influence of other species or from individuals of the same species that might have been present. Although a relatively wide variety of explanatory variables were included in the BRT models, model misspecification, including unexplored niche variables could have skewed model fit and performance. Burn variables were added to the BRT models, but in the analysis of diversity and community similarity no attempt was made to define how recently or how often a site had been burned prior to the study year. Even if a specific site was identified as a *Burn* site in previous years, setting the burned area requirement at a minimum of 50% means that a different portion of that stop's buffer might have burned in any case. Burning may also have occurred outside of the stop buffer, but close enough to impact species present at the stop itself. Finally, no information was available regarding the date burning occurred at a particular stop; if a site was burned just prior to the annual BBS count, a different avian community might be present compared to that at a site where vegetation had more time to recover postburn.

The BRT models created in this study would likely have shown improved performance by including explanatory variables for mowing and grazing regimes. Subdividing the "Woodland" category to include woody vegetation of various types and densities would likely improve model results, particularly for shrub-woodland species like Bell's Vireo. This might be accomplished by adding remotely sensed variables such as image texture or normalized difference vegetation index (NDVI), or by using higher resolution land cover data to more accurately delineate woody vegetation, including cedar and juniper encroachment. To reduce the

overall number of variables, some categories could be combined. For instance, a repeat study could use only the combined cropland variable. Grassland variables for warm season, cool season, and total grassland variables could also be combined into a single categorical variable, assigning actual cover percentages to low, medium, and high levels. Terrain variables could also be reduced in number and be converted into categorical variables rather than using raw values.

Future Research

BRT models could easily be expanded to compare changes in relative variable importance for selected species across short, mid-, and tallgrass prairies. For individual species present in grasslands and forests, BRT models like those developed in this study could be used to determine whether that particular species responds differently to fire in grasslands versus that in forests. Repeating the BRT models using a response variable based on vital rates response, such as nest success, biomass, etc., instead of occurrence, might more accurately reflect habitat quality instead of simply habitat use, and possibly suggest whether burning improves habitat or results in an ecological sink (Vickery, et al., 1992). Although the majority of prescribed burns in the study region occur in April, it would be interesting to compare diversity and community composition at sites where burning occurred in different seasons. Both the BRT modeling and diversity comparisons were conducted at a small, BBS stop-level scale, but it would be valuable to extend these studies to a broader landscape scale more applicable to that at which population management decisions are made. Basing a future study at a landscape scale would also allow researchers to determine whether the BBS routes in current use are reflective of the land cover patterns and burn regimes present in the larger landscape.

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APPENDICES

Appendix 1: Summary of annual survey statistics

Appendix 2: Boosted regression tree model parameters and results

Appendix 3: Area under the Receiver Operating Characteristic curves for focal species models

Appendix 4: Relative variable influence list for focal species models

Appendix 5: Partial dependence plots for focal species models

Appendix 6: All species list with species codes, scientific names, and relative abundances

Appendix 7: Sample-based rarefaction curves for all study years

Appendix 8: Diversity statistics

Appendix 9: Analysis of similarity (ANOSIM) plots for all study years

Appendix 10: Nonmetric multidimensional scaling (NMDS) plots for all study years

APPENDIX 1: Annual survey statistics for all routes examined.

Route	Observer	Year	Month	Day	Start Wind	End Wind	RteHours	Richness	Abundance
Ellinor	1120043	2000	6	18	1	2	4:41	48	477
	1120043	2001	6	17	1	3	4:45	50	441
	1120043	2002	6	21	2	3	4:45	52	486
	1120043	2003	6	13	2	1	4:44	49	479
	1120043	2004	6	19	3	2	4:41	50	355
	1120043	2005	6	21	1	2	4:46	46	406
	1120043	2006	6	10	2	2	4:37	47	370
	1120043	2007	6	16	1	2	5:06	54	397
	1120043	2008	6	24	3	3	5:21	48	347
	1120043	2009	6	22	3	2	5:05	47	343
	1120043	2010	6	19	1	2	4:47	44	329
Lapland	1080094	2000	6	25	0	1	4:27	52	742
	1080094	2001	7	1	0	0	4:16	51	725
	1080094	2004	6	19	2	1	4:16	37	462
	1080094	2005	6	18	0	2	4:16	49	578
	1080094	2007	6	24	0	1	4:40	47	485
	1080094	2008	7	7	1	1	4:12	40	429
	1080094	2009	6	27	0	2	4:05	40	559
	1080094	2010	6	15	2	2	4:15	41	493
Lincolnville	980479	2003	6	18	0	1	4:23	59	1070
	980479	2004	6	23	1	2	4:15	61	955
	980479	2005	6	15	0	1	4:35	59	1182
	980479	2006	6	28	0	1	4:20	58	1059
	980479	2007	6	9	1	2	4:29	57	958
	980479	2008	5	29	2	3	4:25	61	913
	980479	2009	5	30	1	2	4:23	59	948
	980479	2010	6	15	2	1	4:30	64	989
Longton	1080094	2000	5	29	0	2	4:20	53	601
	1080094	2001	6	24	0	2	4:01	53	662
	1080094	2002	7	7	1	1	4:12	48	597
	1080094	2003	6	7	0	2	4:31	47	642
	1080094	2005	6	5	0	0	4:23	45	562
	1080094	2007	6	20	2	1	5:01	48	481
	1080094	2008	6	28	1	0	5:09	39	329
	1080094	2009	6	13	3	3	4:10	46	454
	1080094	2010	6	11	3	3	4:09	38	411
Olsburg	1140412	2001	6	8	0	2	4:43	71	925
	1140412	2002	6	9	1	3	4:47	71	797
	1140412	2003	6	14	0	1	4:15	76	858

	1140412	2004	6	5	1	2	4:19	69	776
	1140412	2006	6	7	0	2	4:02	77	791
	1140412	2007	6	9	0	2	4:12	72	721
	1140412	2008	6	29	1	5	4:08	66	776
	1140412	2009	5	31	0	3	4:12	68	779
Reece	1110111	2001	6	17	2	3	4:03	54	639
	1110111	2002	6	15	3	1	3:58	53	740
	1110111	2003	6	15	0	1	3:56	53	744
	1110111	2004	6	19	0	3	4:02	59	761
	1060330	2008	6	9	1	2	5:23	63	687
	1060330	2009	6	5	0	2	5:36	66	853
	1060330	2010	6	15	1	2	4:51	56	764
Wreford	1110081	2000	6	18	0	1	4:12	67	1426
	1110081	2001	6	23	2	3	4:08	67	1022
	1110081	2002	6	23	2	2	4:14	64	1142
	1110081	2003	6	8	0	3	4:17	71	1291
	1110081	2004	6	29	1	1	4:18	62	1480
	1110081	2005	6	5	2	2	4:07	73	1400
	1110081	2006	6	18	2	2	3:59	68	1466
	1110081	2007	6	2	1	3	4:05	66	1440
	1110081	2008	6	1	1	2	4:18	71	1478
	1110081	2009	6	21	2	4	4:10	64	1179
	1110081	2010	6	20	1	3	4:09	66	1272

APPENDIX 2: BRT model parameters and results for the simplified model (30 predictors) for each focal species model.

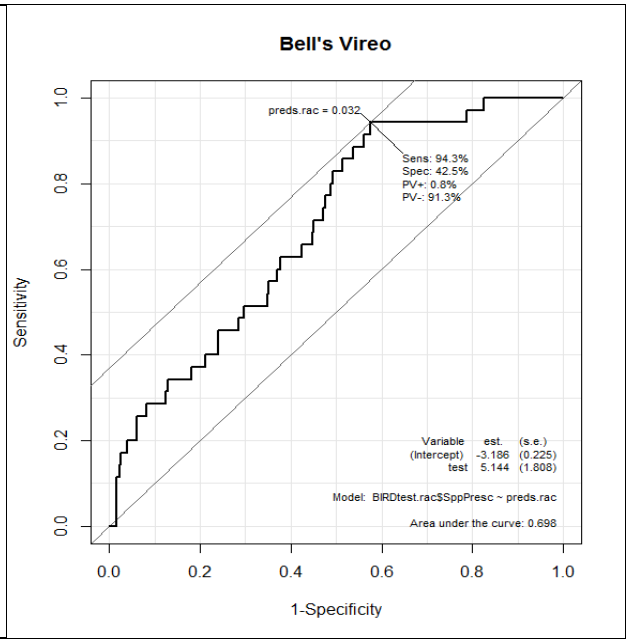
					Deviance		ROC score		Pseudo
Species*	**Records**	**tc**	**lr**	**# trees**	**CV**	**CV.SE**	**CV**	**CV.SE**	**R2**
BEVI	637	4	0.0005	5500	0.439	0.021	0.719	0.04	8.086
BHCO	725	5	0.001	3403	1.152	0.074	0.756	0.018	15.814
CARW	537	2	0.001	3223	0.587	0.023	0.743	0.033	9.991
CONI	675	4	0.001	4103	0.524	0.029	0.824	0.029	21.424
DICK	775	10	0.00075	3730	0.839	0.029	0.806	0.017	20.31
EAME	775	10	0.0005	3618	1.066	0.034	0.812	0.016	23.128
FISP	625	6	0.00025	7850	0.657	0.024	0.781	0.027	17.346
GRSP	725	10	0.0025	6028	0.882	0.039	0.819	0.02	23.902
MODO	775	6	0.00075	4470	1.18	0.028	0.745	0.019	13.733
NOBO	775	10	0.0005	5039	1.129	0.029	0.771	0.016	16.82
RHWO	625	6	0.0005	4845	0.344	0.017	0.742	0.043	8.466
RWBL	775	6	0.00075	5848	1.081	0.031	0.792	0.015	20.128
UPSA	738	6	0.001	4365	0.723	0.034	0.87	0.014	32.675
WEME	325	3	0.001	4773	0.42	0.058	0.94	0.019	51.118
YBCU	775	3	0.001	5240	0.959	0.028	0.773	0.019	14.985

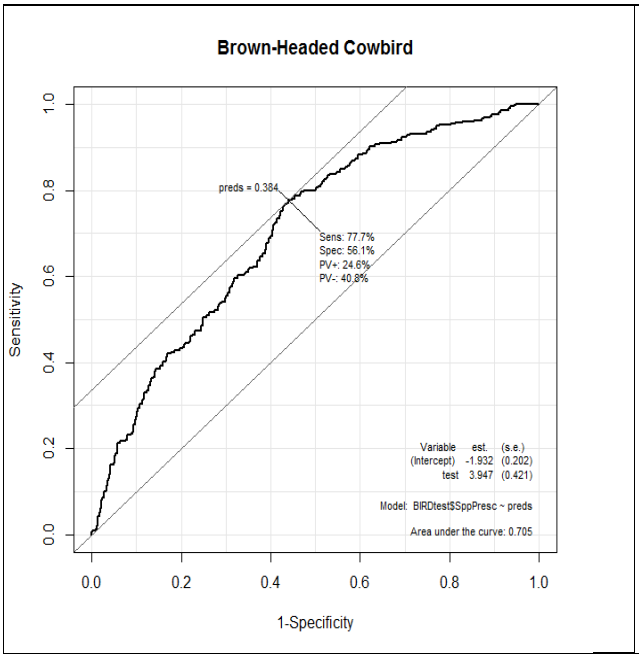
*American Ornithological Union four-letter Alpha Code (Pyle & DeSante, 2014)

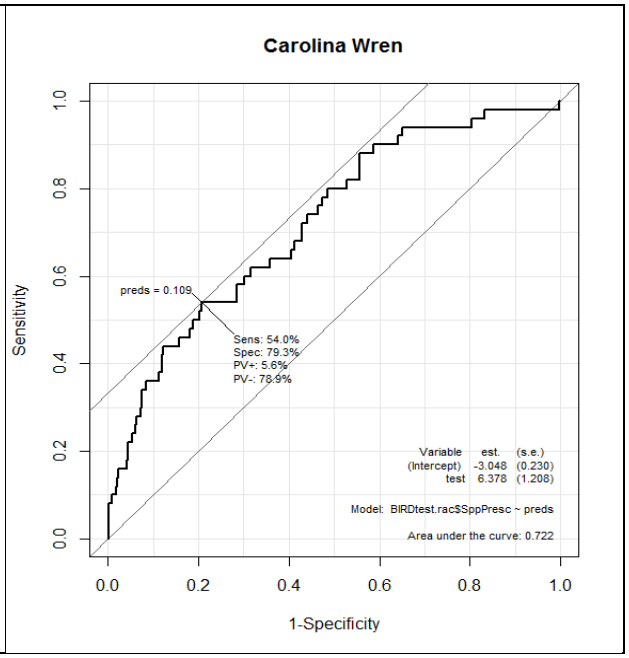
AOU code*	**Common Name**
BEVI	Bell's Vireo
BHCO	Brown-headed Cowbird
CARW	Carolina Wren
CONI	Common Nighthawk
DICK	Dickcissel
EAME	Eastern Meadowlark
FISP	Field Sparrow
GRSP	Grasshopper Sparrow
MODO	Mourning Dove
NOBO	Northern Bobwhite
RHWO	Red-headed Woodpecker
RWBL	Red-winged Blackbird
UPSA	Upland Sandpiper
WEME	Western Meadowlark
YBCU	Yellow-billed Cuckoo

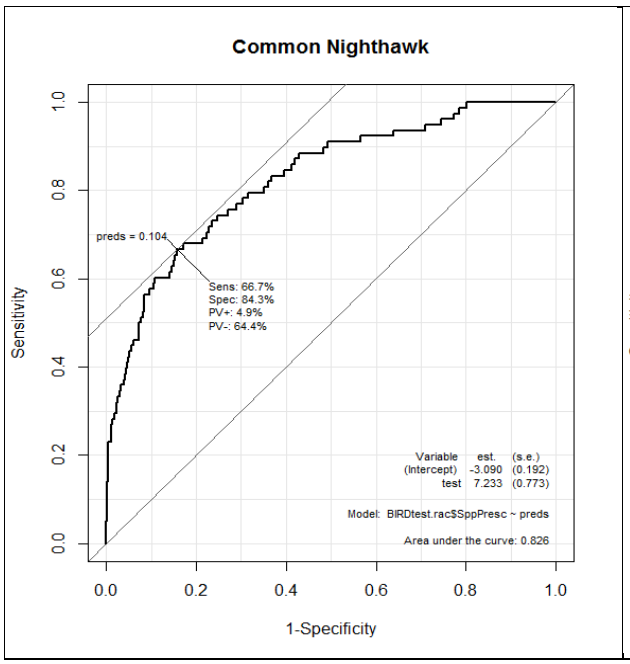
APPENDIX 3: Area under the Receiver Operating Characteristic curves for each focal species, reflecting how well the species model can discriminte between species presence and absence when applied to independant data. Model accuracy, as represented by the ROC score, is roughly analygous to a traditional academic grading system.

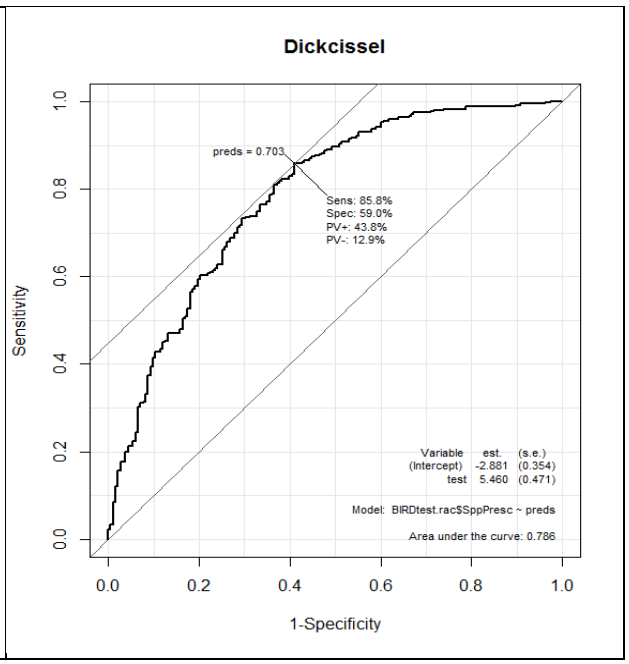
Species Common Name	ROC score
Bell's Vireo	0.698
Brown-headed Cowbird	0.704
Carolina Wren	0.720
Common Nighthawk	0.828
Dickcissel	0.819
Eastern Meadowlark	0.802
Field Sparrow	0.820
Grasshopper Sparrow	0.802
Mourning Dove	0.690
Northern Bobwhite	0.768
Red-headed Woodpecker	0.545
Red-winged Blackbird	0.727
Upland Sandpiper	0.861
Western Meadowlark	0.886
Yellow-billed Cuckoo	0.719

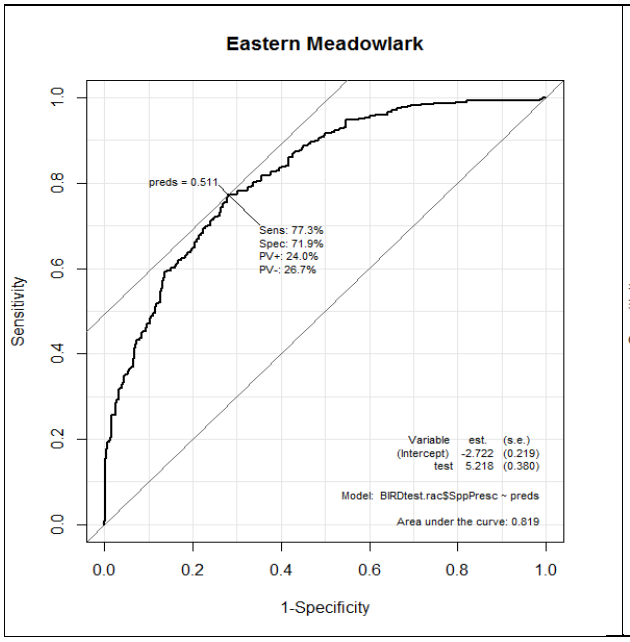


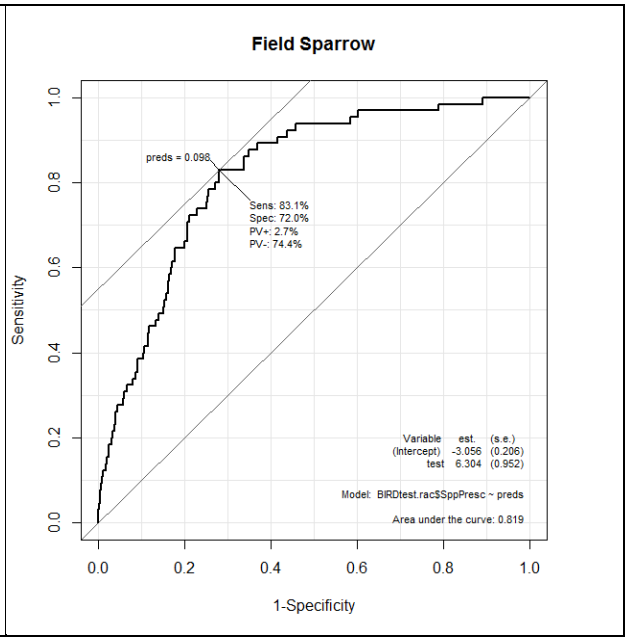


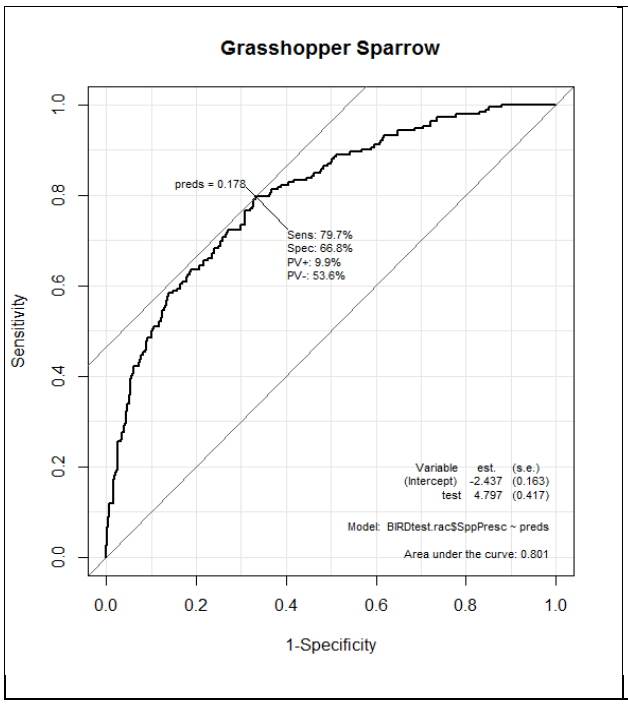


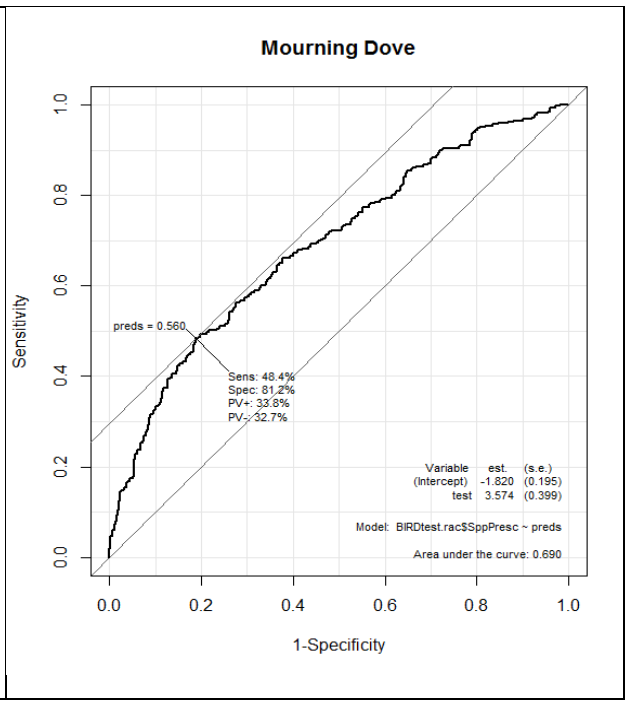

Common Nighthawk
Sensitivity
1-Specificity
preds = 0.104
Sens: 66.7%
Spec: 84.3%
PV+: 4.9%
PV-: 64.4%
Variable est. (s.e.)
(Intercept) -3.090 (0.192)
test 7.233 (0.773)
Model: BIRDtest.rac$SppPresc ~ preds
Area under the curve: 0.826

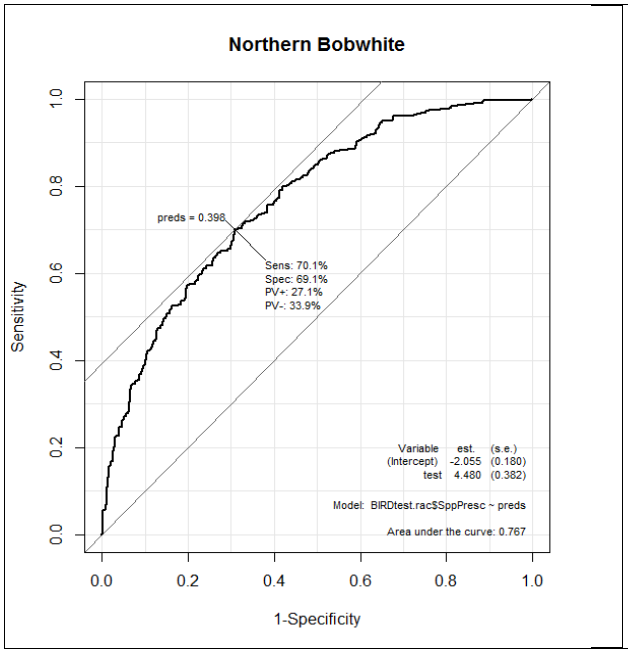

Dickcissel
Sensitivity
1-Specificity
preds = 0.703
Sens: 85.8%
Spec: 59.0%
PV+: 43.8%
PV-: 12.9%
Variable est. (s.e.)
(Intercept) -2.881 (0.354)
test 5.460 (0.471)
Model: BIRDtest.rac$SppPresc ~ preds
Area under the curve: 0.786

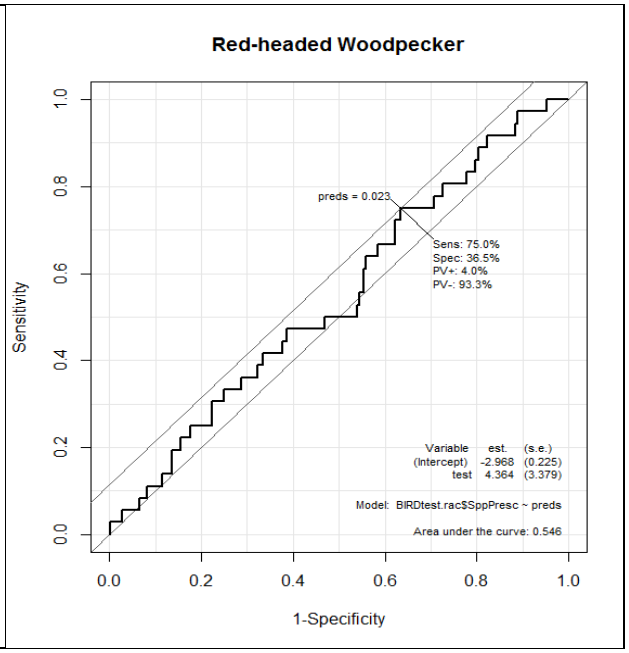

Eastern Meadowlark
Sensitivity
1-Specificity
preds = 0.511
Sens: 77.3%
Spec: 71.9%
PV+: 24.0%
PV-: 26.7%
Variable est. (s.e.)
(Intercept) -2.722 (0.219)
test 5.218 (0.380)
Model: BIRDtest.rac$SppPresc ~ preds
Area under the curve: 0.819

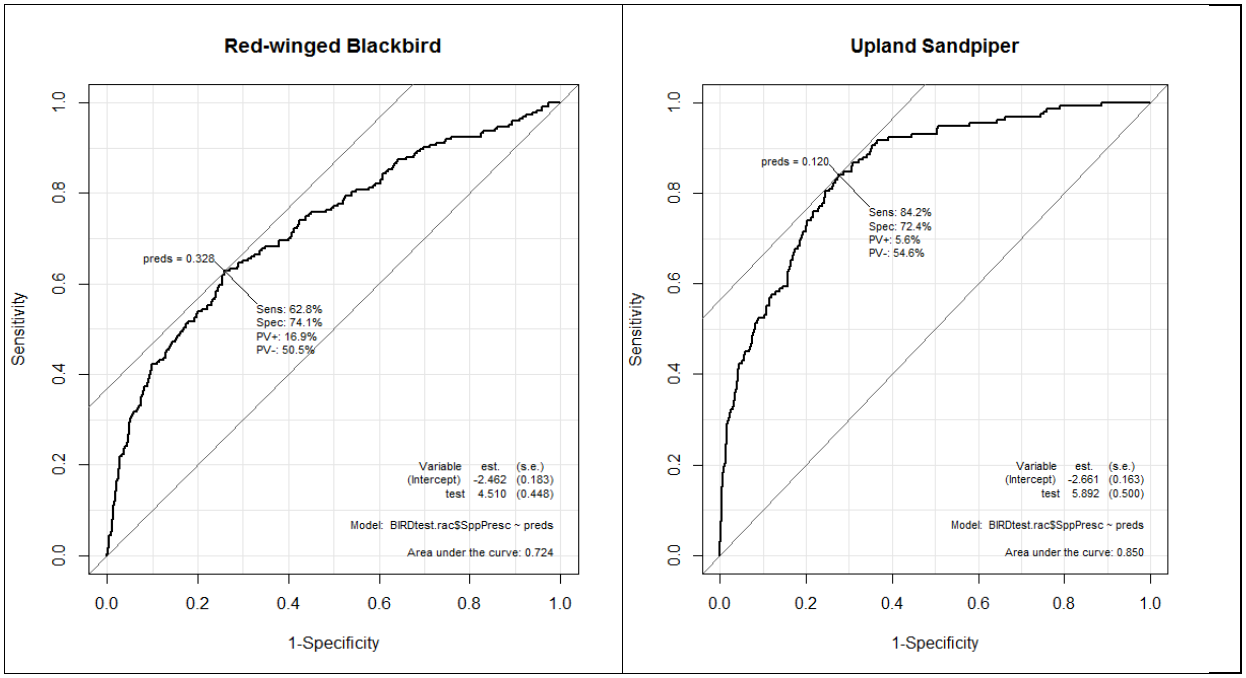

Field Sparrow
Sensitivity
1-Specificity
preds = 0.098
Sens: 83.1%
Spec: 72.0%
PV+: 2.7%
PV-: 74.4%
Variable est. (s.e.)
(Intercept) -3.056 (0.206)
test 6.304 (0.952)
Model: BIRDtest.rac$SppPresc ~ preds
Area under the curve: 0.819

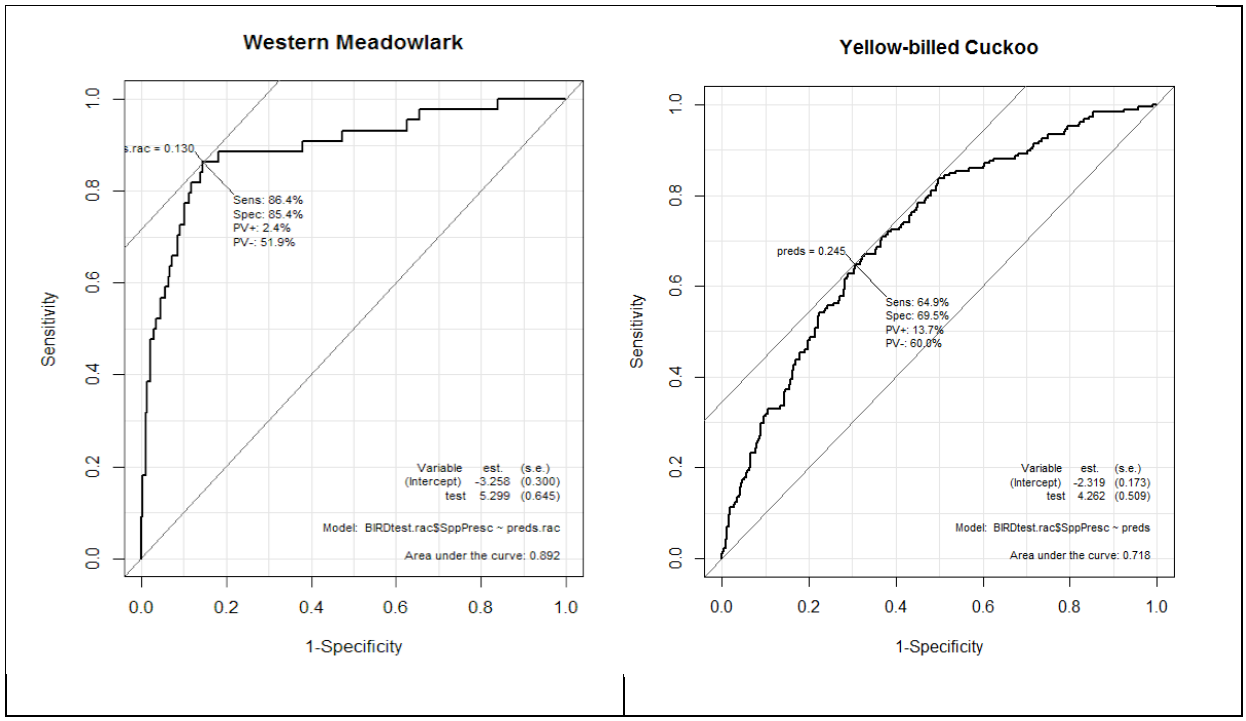

Grasshopper Sparrow
preds = 0.178
Sens: 79.7%
Spec: 66.8%
PV+: 9.9%
PV-: 53.6%
Variable est. (s.e.)
(Intercept) -2.437 (0.163)
test 4.797 (0.417)
Model: BIRDtest.rac$SppPresc ~ preds
Area under the curve: 0.801
Sensitivity
1-Specificity
0.0
0.2
0.4
0.6
0.8
1.0


Mourning Dove
preds = 0.560
Sens: 48.4%
Spec: 81.2%
PV+: 33.8%
PV-: 32.7%
Variable est. (s.e.)
(Intercept) -1.820 (0.195)
test 3.574 (0.399)
Model: BIRDtest.rac$SppPresc ~ preds
Area under the curve: 0.690
Sensitivity
1-Specificity
0.0
0.2
0.4
0.6
0.8
1.0


Northern Bobwhite
preds = 0.398
Sens: 70.1%
Spec: 69.1%
PV+: 27.1%
PV-: 33.9%
Variable est. (s.e.)
(Intercept) -2.055 (0.180)
test 4.480 (0.382)
Model: BIRDtest.rac$SppPresc ~ preds
Area under the curve: 0.767
Sensitivity
1-Specificity
0.0
0.2
0.4
0.6
0.8
1.0


Red-headed Woodpecker
preds = 0.023
Sens: 75.0%
Spec: 36.5%
PV+: 4.0%
PV-: 93.3%
Variable est. (s.e.)
(Intercept) -2.968 (0.225)
test 4.364 (3.379)
Model: BIRDtest.rac$SppPresc ~ preds
Area under the curve: 0.546
Sensitivity
1-Specificity
0.0
0.2
0.4
0.6
0.8
1.0


Red-winged Blackbird
Sensitivity
1-Specificity
preds = 0.328
Sens: 62.8%
Spec: 74.1%
PV+: 16.9%
PV-: 50.5%
Variable est. (s.e.)
(Intercept) -2.462 (0.183)
test 4.510 (0.448)
Model: BIRDtest.rac$SppPresc ~ preds
Area under the curve: 0.724
Upland Sandpiper
preds = 0.120
Sens: 84.2%
Spec: 72.4%
PV+: 5.6%
PV-: 54.6%
Variable est. (s.e.)
(Intercept) -2.661 (0.163)
test 5.892 (0.500)
Model: BIRDtest.rac$SppPresc ~ preds
Area under the curve: 0.850


Western Meadowlark
Sensitivity
1-Specificity
s.rac = 0.130
Sens: 86.4%
Spec: 85.4%
PV+: 2.4%
PV-: 51.9%
Variable est. (s.e.)
(Intercept) -3.258 (0.300)
test 5.299 (0.645)
Model: BIRDtest.rac$SppPresc ~ preds.rac
Area under the curve: 0.892
Yellow-billed Cuckoo
preds = 0.245
Sens: 64.9%
Spec: 69.5%
PV+: 13.7%
PV-: 60.8%
Variable est. (s.e.)
(Intercept) -2.319 (0.173)
test 4.262 (0.509)
Model: BIRDtest.rac$SppPresc ~ preds
Area under the curve: 0.718

APPENDIX 4: Relative variable influence for focal species simplified models. Variable abbreviations are in Chapter 2, Table 3.

Bell's Vireo		**Brown-headed Cowbird**		**Carolina Wren**	
Variable	Influence	Variable	Influence	Variable	Influence
RTEsection	16.4131	RTEsection	18.4712	WoodEdge	12.4484
BHCORelN	7.9399	Observer	16.3162	Pspg_sd	9.0107
Corn	6.4771	MeanElev	11.4211	SPI06_Apr	8.1002
SlopePosNdx	5.4162	Burn_Yr2	3.8223	WarmGrass	6.8865
Y2	4.0649	RteHours	3.6298	RTEsection	6.5612
Burn_Yr2	3.5978	CH_Inter50	3.0413	Woodland	5.6841
MeanSlope	3.3123	AvgPDSI_y2	2.7927	Observer	4.3160
SDslope	3.3008	LULC_H	2.7648	BHCORelN	3.6284
WarmGrass	3.2882	X1	2.7449	Pspg_tot	3.5956
PMar_pctn	2.8960	StartWind	2.7126	MeanSlope	3.5183
RACvect	2.8493	Burn_Yr1	2.4875	MeanElev	3.3202
Pwin_tot	2.7920	Pspg_sd	2.1404	ERR30	2.9958
CoreHab	2.7493	CH_maxpch	2.1122	SmrTmin	2.8762
CRP	2.6752	CoolGrass	1.9989	Pwatyr_tot	2.4676
SPI06_May	2.6321	WinTmax	1.8069	TRASP	2.2868
ERR30	2.6309	TRASP	1.7804	Corn	2.1992
Pwin_sd	2.4988	SmrTmin	1.7791	AvgPDSI_y2	2.0333
TRASP	2.4669	SDslope	1.7020	Psmr_sd	1.9352
X1	2.4018	PMar_pctn	1.6466	CH_maxpch	1.8534
Water	2.3731	CoreHab	1.6259	CH_Inter50	1.8055
MeanElev	2.0631	Woodland	1.5208	CoolGrass	1.5613
SpgTmin0	1.9111	MeanSlope	1.4196	LULC_H	1.5494
CH_Inter50	1.8062	WinTmin	1.3939	Burn_Yr2	1.5282
Psmr_tot	1.7899	PMar_sd	1.3624	Pwin_sd	1.4784
SpgTmean	1.7286	WoodEdge	1.3416	Water	1.3937
WoodEdge	1.6437	Psmr_tot	1.3372	Psmr_tot	1.2938
AllCrops	1.5946	Day	1.2880	Pann_tot	1.1456
LULC_H	1.5777	Water	1.2700	Burn_Yr1	1.0615
Psmr_sd	1.5744	Pwin_sd	1.1853	Pwin_tot	0.7811
AvgPDSI_y	1.5352	Psmr_sd	1.0844	RACvect	0.6800

Common Nighthawk	
Variable	Influence
RTEsection	21.6394
SlopePosNdx	8.2601
Burn_Yr1	7.6292
CH_Inter50	6.3992
MeanElev	4.8638
ERR30	3.9794
SDslope	3.8466
Burn_Yr2	3.5225
PMar_pctn	3.3060
Day	3.0802
SmrTmin	3.0278
Observer	2.7532
CoreHab	2.1140
Psmr_sd	2.1054
X1	1.9190
SmrTmean	1.7645
ZNDX_Mar	1.7169
RACvect	1.6991
WarmGrass	1.6710
MeanSlope	1.6338
Pwatyr_tot	1.5996
Woodland	1.5881
WinTmax	1.5353
TRASP	1.3319
CH_maxpch	1.2766
RteHours	1.2467
SpgTmean	1.1901
SpgTmax	1.1633
PMar_sd	1.1102
WinTmean	1.0268

Dickcissel	
Variable	Influence
RTEsection	11.5283
Woodland	11.0127
WoodEdge	10.9466
MeanSlope	3.7835
Observer	3.3398
Burn_Yr2	3.3164
TRASP	3.1811
CH_Inter50	3.1250
SDslope	2.9571
Pspg_sd	2.8306
Y2	2.7270
Pwin_tot	2.7190
StartWind	2.7110
CoolGrass	2.5040
LULC_H	2.4337
Burn_Yr1	2.4083
CoreHab	2.3889
SmrTmin	2.2944
WinTmin	2.2933
MeanElev	2.2885
Pspg_tot	2.1570
SlopePosNdx	2.0432
SpgTmin	2.0384
AllElse	2.0170
PMar_pctn	2.0059
Corn	1.9407
CH_maxpch	1.8570
PMar_sd	1.8400
WinTmax	1.7877
RACvect	1.5240

Eastern Meadowlark	
Variable	Influence
CoreHab	9.8851
CH_Inter50	9.5482
RTEsection	7.3566
Observer	5.6835
MeanElev	4.8702
WoodEdge	4.8001
Woodland	4.0457
Soybeans	3.9616
BHCOrelN	3.7466
ERR30	3.4302
MeanSlope	3.1726
Y2	2.9123
LULC_H	2.7675
TRASP	2.7347
Day	2.7309
X1	2.6054
Burn_Yr1	2.4336
WarmGrass	2.3834
SDslope	2.2840
Pwin_sd	2.1917
SlopePosNdx	2.1240
Burn_Yr2	2.0340
Psmr_tot	1.6540
WinTmean	1.5949
CH_maxpch	1.5881
WinTmean0	1.5430
SmrTmax	1.5313
SpgTmax	1.4980
PMar_pctn	1.4709
RteHours	1.4180

Field Sparrow		**Grasshopper Sparrow**		**Mourning Dove**	
Variable	Influence	Variable	Influence	Variable	Influence
RTEsection	17.5044	CH_Inter50	17.0977	X1	16.9635
Observer	11.6304	WarmGrass	12.7143	RTEsection	14.4413
MeanSlope	11.2479	RTEsection	8.6245	TRASP	5.2692
WarmGrass	6.3514	Burn_Yr1	5.5624	Observer	5.2249
CH_Inter50	3.5875	MeanElev	4.6504	MeanSlope	4.8956
Burn_Yr1	3.4533	SlopePosNdx	3.5977	Y2	4.4181
WoodEdge	3.2737	X1	3.5771	SlopePosNdx	3.6687
Pspg_tot	3.0453	SDslope	3.0524	SmrTmax	3.5084
SpgTmin	2.7636	Observer	2.7752	Pwin_sd	2.9486
X1	2.5325	WinTmin	2.6063	WoodEdge	2.8743
CH_maxpch	2.2397	TRASP	2.4450	Pann_tot	2.7468
RACvect	2.1825	Pspg_tot	2.3831	MeanElev	2.7356
CoreHab	2.1081	CH_maxpch	2.3760	WarmGrass	2.6900
SmrTmax	2.0350	CoreHab	2.3747	LULC_H	2.3107
TRASP	1.9995	Burn_Yr2	2.0483	SDslope	2.1851
Burn_Yr	1.9516	Y2	1.9058	Pwatyr_tot	1.9940
Pspg_sd	1.8582	avgPDSI_y1	1.8970	ERR30	1.8686
Burn_Yr2	1.8239	WoodEdge	1.7816	CoolGrass	1.8529
LULC_H	1.8208	SpgTmean	1.7133	Pspg_tot	1.7204
WinTmax	1.7802	Pwin_tot	1.6739	Psmr_sd	1.6603
PMar_sd	1.7199	RACvect	1.6737	BHCOrelN	1.5778
SlopePosNdx	1.6365	Burn_Yr	1.6661	Burn_Yr	1.5734
BHCOrelN	1.6157	Pann_tot	1.6255	Burn_Yr2	1.5476
SPI06_Apr	1.6140	SmrTmin	1.5871	SpgTmin	1.5432
RteHours	1.5233	SmrTmax	1.5137	CoreHab	1.4157
Woodland	1.4272	ERR30	1.4818	Burn_Yr1	1.4135
Y2	1.3753	BHCOrelN	1.4816	Pwin_tot	1.3431
CRP	1.3735	Psmr_sd	1.3874	EndWind	1.2738
MeanElev	1.2835	WinTmax	1.3774	SpgTmean	1.2533
SDSlope	1.2414	SpgTmax	1.3489	WinTmax	1.0814

Northern Bobwhite		**Red-headed Woodpecker**		**Red-winged Blackbird**	
Variable	Influence	Variable	Influence	Variable	Influence
CoreHab	7.6583	LULC_H	12.0124	MeanSlope	15.2786
RACvect	7.0688	Soybean	8.2582	WoodEdge	8.0851
CH_Inter50	6.8977	RTEsection	7.1370	Woodland	8.0402
RteHours	4.9772	WinTmean0	5.0370	TRASP	7.0313
Burn_Yr1	4.8179	CoreHab	4.7273	X1	4.8865
ERR30	4.4495	Woodland	4.4063	SlopePosNdx	4.7854
SlopePosNdx	3.6425	ERR30	4.2441	Water	4.4814
Y2	3.6354	AvgPDSI_y2	4.0878	WarmGrass	4.1147
Observer	3.4174	TRASP	3.9739	Burn_Yr1	3.7392
MeanElev	3.0850	CoolGrass	3.9666	SDslope	3.7214
RTEsection	3.0468	SlopePosNdx	3.8038	ERR30	2.8532
WinTmin	3.0286	CH_maxpch	3.7343	RACvect	2.5794
Woodland	2.9311	RACvect	3.4824	Psmr_sd	2.3912
X1	2.9274	MeanSlope	2.5759	SmrTmean	2.1971
WinTmean	2.8267	Pann_tot	2.3407	MeanElev	2.0715
Psmr_sd	2.8241	SpgTmin	2.3223	CoolGrass	2.0153
SmrTmax	2.7012	SpgTmax	2.2654	SpgTmax	1.9595
WinTmean0	2.6689	Burn_Yr2	2.0886	CoreHab	1.9116
Pwin_sd	2.5979	Burn_Yr1	2.0790	SpgTmin	1.8198
MeanSlope	2.5248	MeanElev	1.9706	Pann_tot	1.7830
PMar_pctn	2.4500	Psmr_tot	1.8882	ZNDX_Mar	1.7632
LULC_H	2.3930	SpgTmin0	1.8714	BHCOrelN	1.7445
BHCOrelN	2.3808	SmrTmean	1.8435	SpgTmin0	1.6716
SmrTmean	2.3745	X1	1.7282	CH_maxpch	1.6234
SpgTmax	2.3117	WinTmin	1.6605	WinTmax	1.5219
TRASP	2.2034	Pwin_sd	1.5570	CH_Inter50	1.4703
WarmGrass	2.1691	PMar_sd	1.4528	Soybean	1.4000
Burn_Yr2	2.1162	PMar_pctn	1.4266	Pwatyr_tot	1.1710
WinTmax	2.0410	WinTmax	1.2502	Alfalfa	0.9739
CH_maxpch	1.8331	Pspg_tot	0.8079	Day	0.9150

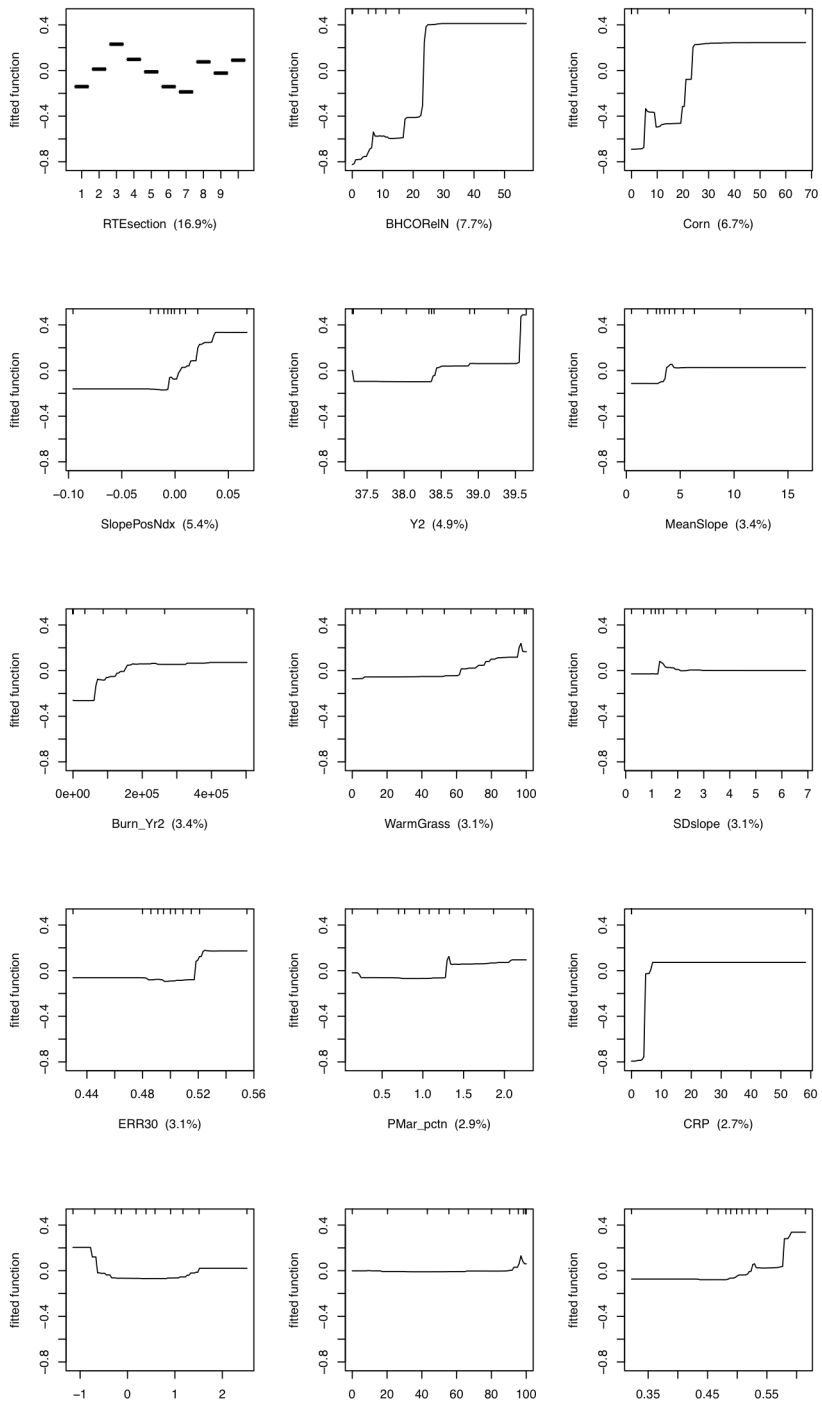
Upland Sandpiper	
Variable	Influence
CH_maxpch	17.9281
RTEsection	8.5414
MeanElev	8.2822
Burn_Yr1	6.8963
CH_Inter50	6.5570
RACvect	4.8101
Burn_Yr2	3.0926
ERR30	2.9797
Psmr_sd	2.6864
WoodEdge	2.2908
Pann_tot	2.2839
Burn_Yr	2.2403
SpgTmax	2.2174
Pspg_tot	2.1540
Pwatyr_tot	2.1303
WarmGrass	2.1076
Woodland	2.0798
X1	1.9978
TRASP	1.9192
CoreHab	1.8399
SlopePosNdx	1.6905
AllCrops	1.6692
Pwin_sd	1.6244
ZNDX_Mar	1.5835
SPI06_Apr	1.5134
Day	1.4892
PMar_sd	1.4751
SmrTmean	1.3641
SDslope	1.3223
Observer	1.2334

Western Meadowlark	
Variable	Influence
MeanSlope	24.7966
SDslope	13.7844
RTEsection	11.4948
ERR30	9.3348
MeanElev	6.1717
Woodland	3.1818
TRASP	3.1234
Psmr_sd	3.1074
WoodEdge	2.9629
PMar_pctn	2.8429
PMar_sd	2.5171
BHCOrelN	2.2938
WinTmin	1.8817
avgPDSI_y1	1.4196
SpgTmean	1.3058
Burn_Yr1	1.2592
WinTmax	0.9893
SlopePosNdx	0.8282
WinTmean	0.8181
Pspg_tot	0.7554
CoreHab	0.7082
LULC_H	0.5782
CoolGrass	0.5444
SmrTmin	0.5356
avgPDSI_y	0.5326
Day	0.5319
AllCrops	0.5168
WinTmean0	0.4754
SmrTmean	0.4102
Psmr_tot	0.2980

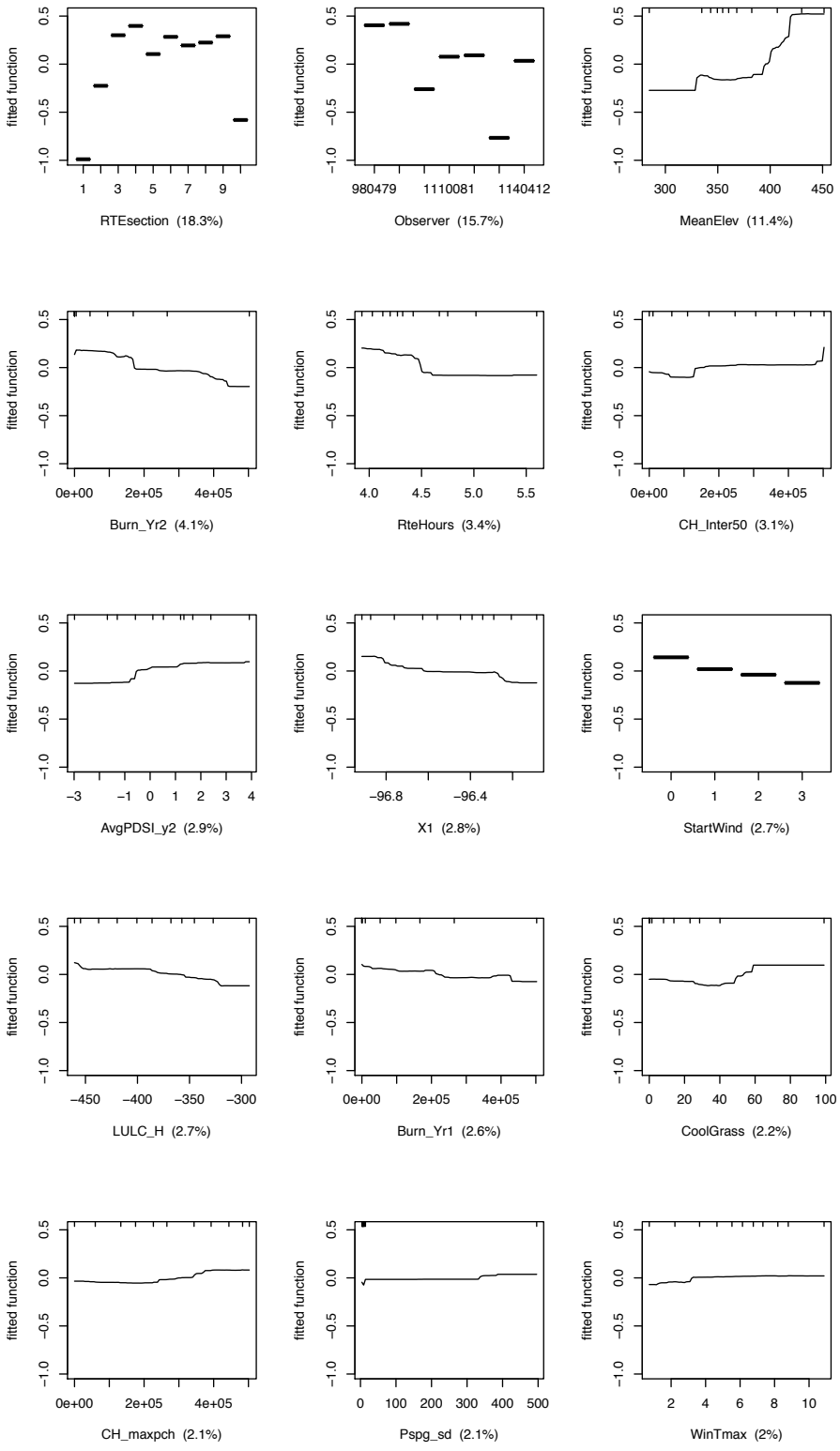
Yellow-billed Cuckoo	
Variable	Influence
WoodEdge	10.4580
RTEsection	7.6875
Observer	7.2022
RteHours	6.8241
SlopePosNdx	5.9445
Pwin_sd	5.9242
MeanSlope	4.2690
EndWind	4.0370
SDslope	3.8310
AvgPDSI_y	3.4374
Y2	3.3844
StartWind	3.1238
CoolGrass	3.0672
WinTmean0	2.5633
WarmGrass	2.5136
PMar_pctn	2.4072
SpgTmin	2.2451
BHCOrelN	2.1976
LULC_H	2.0164
Burn_Yr1	1.8982
Burn_Yr	1.7794
Pspg_sd	1.7319
WinTmin	1.5963
Pwin_tot	1.5954
TRASP	1.5487
Woodland	1.4970
AvgPDSI_y1	1.4324
SpgTmean	1.3893
SpgTmin0	1.2537
CoreHab	1.1444

APPENDIX 5: Partial dependence plots for the fifteen most influential variables for focal species models. Variable names and descriptions can be found in Chapter 2, Table 3.

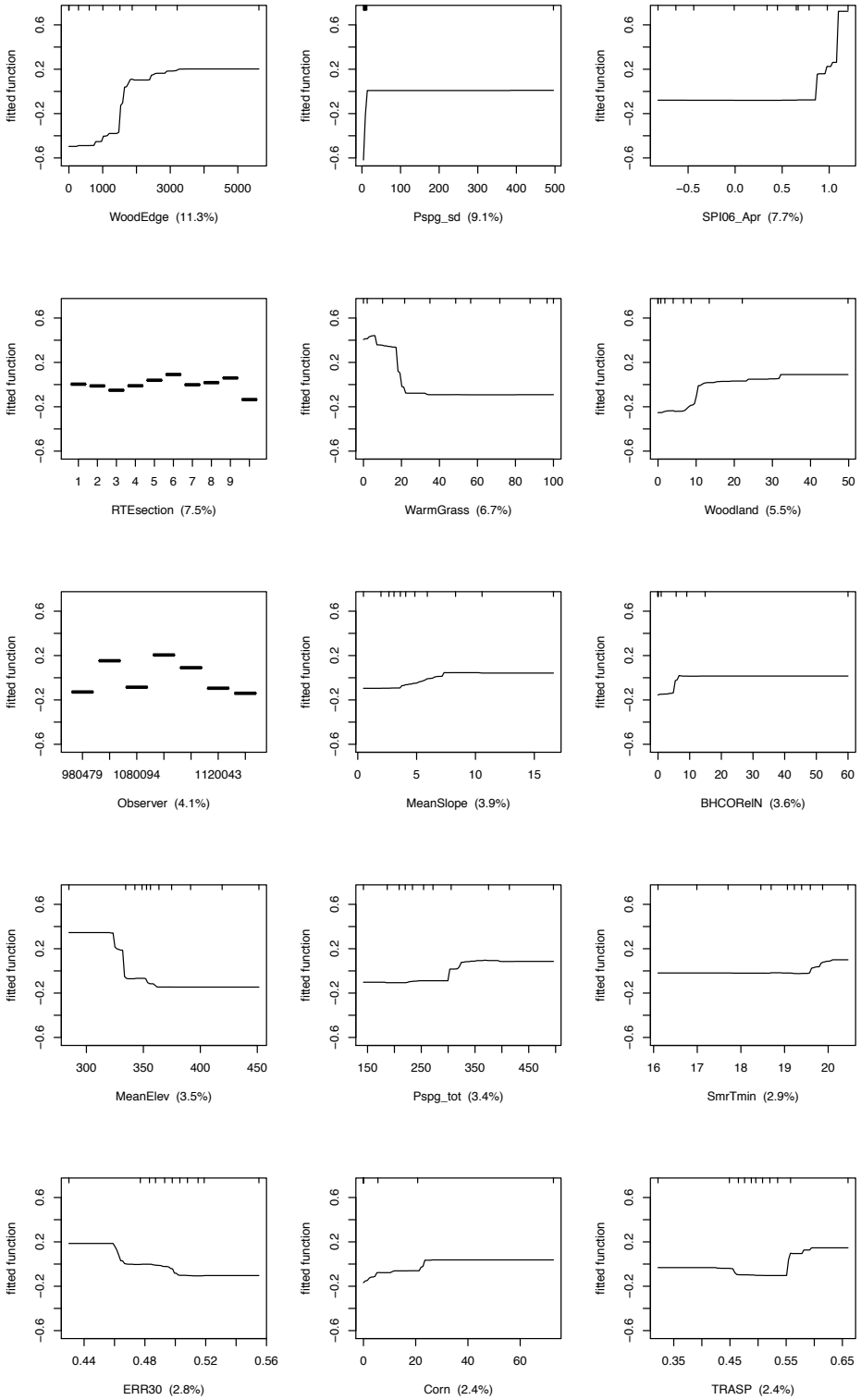
BELL'S VIREO



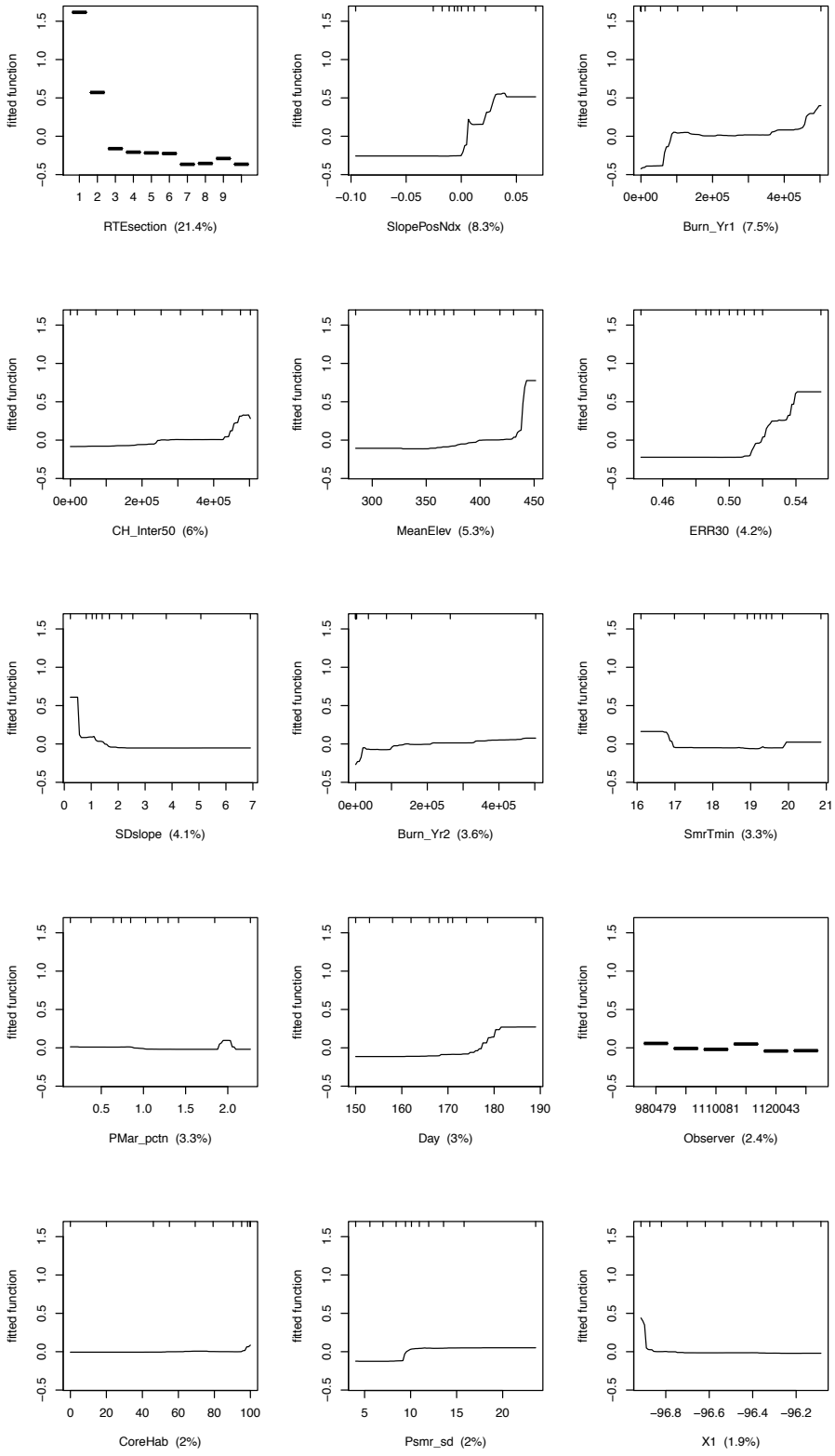
BROWN-HEADED COWBIRD



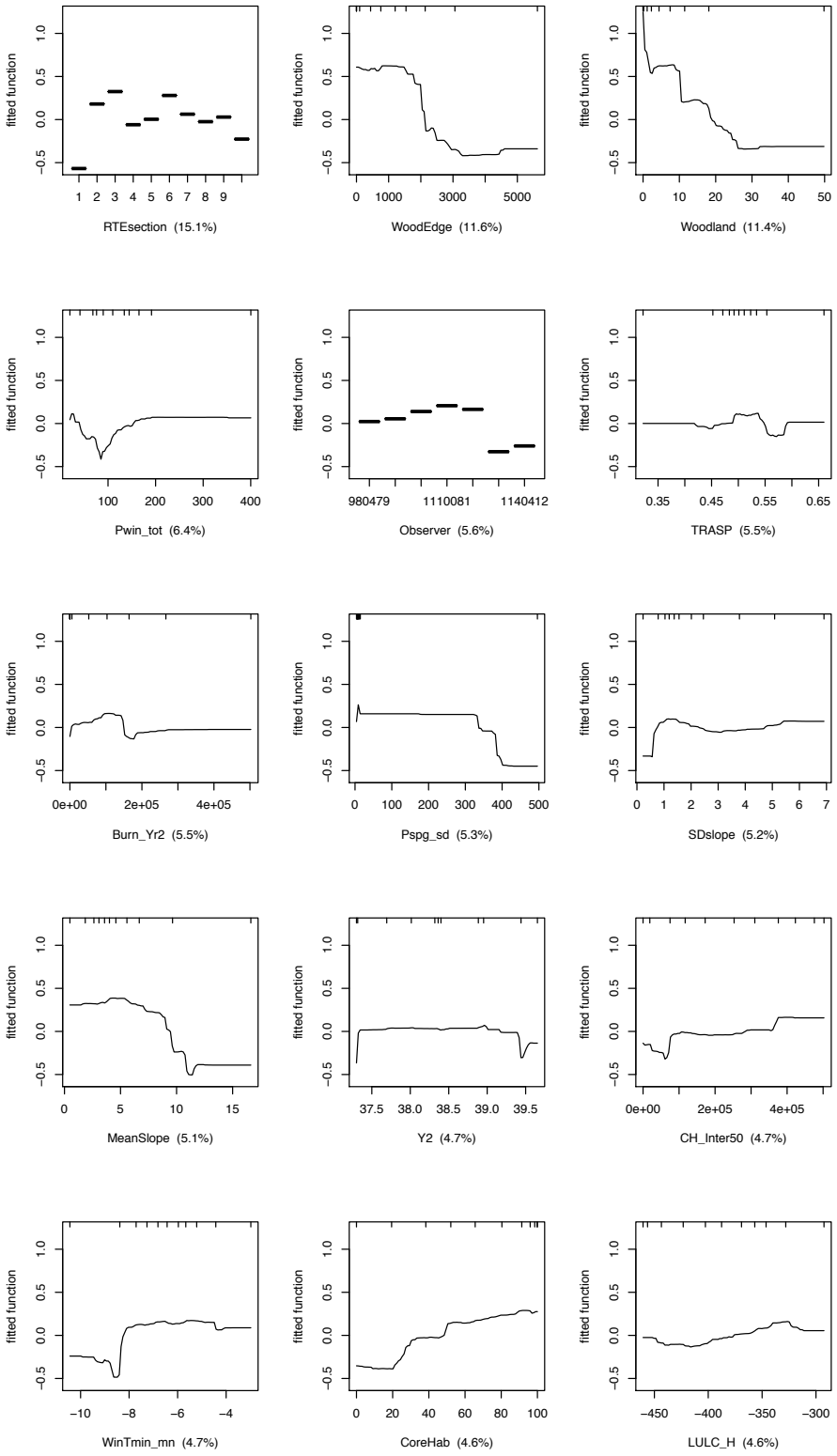
CAROLINA WREN



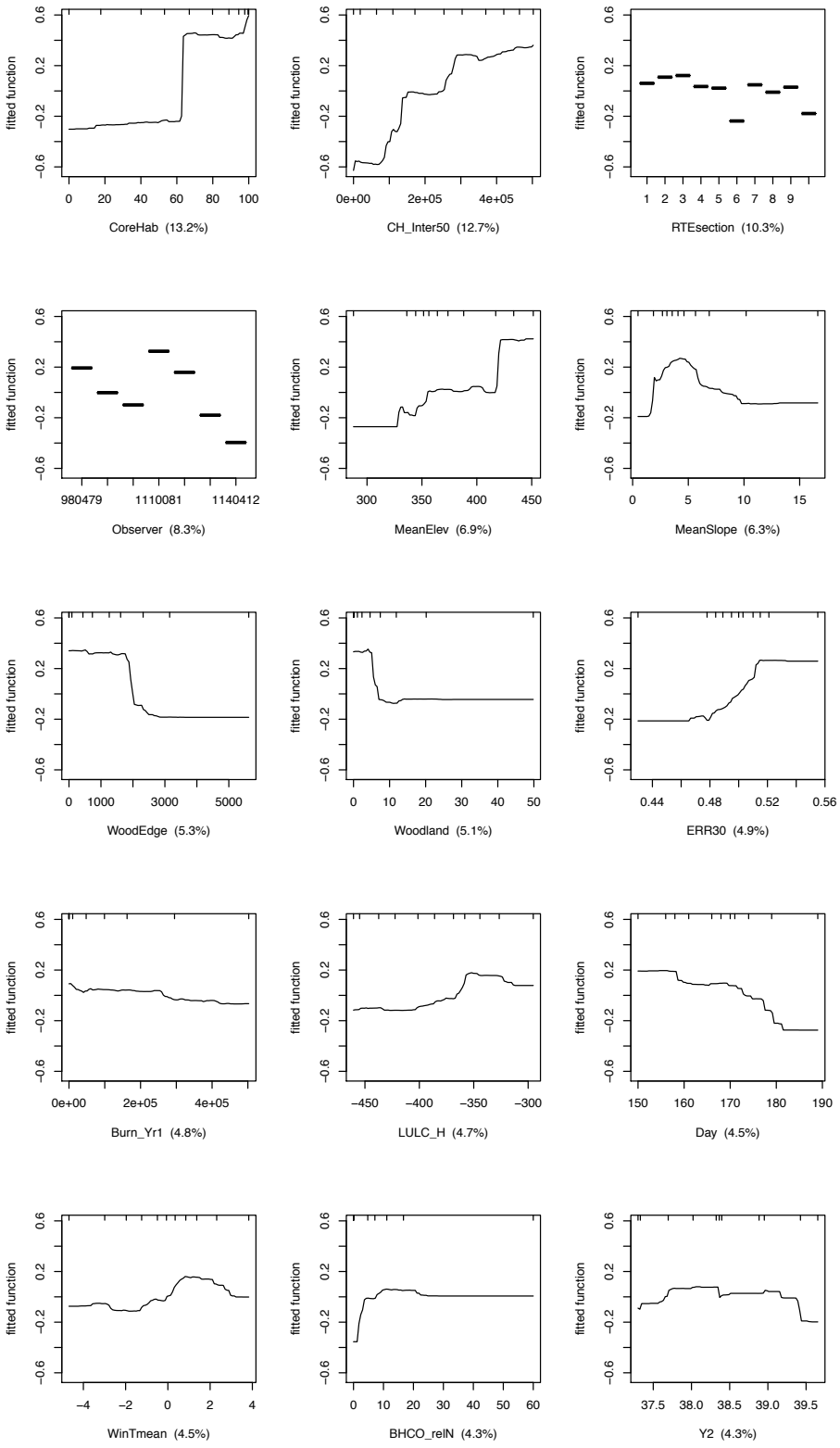
COMMON NIGHTHAWK



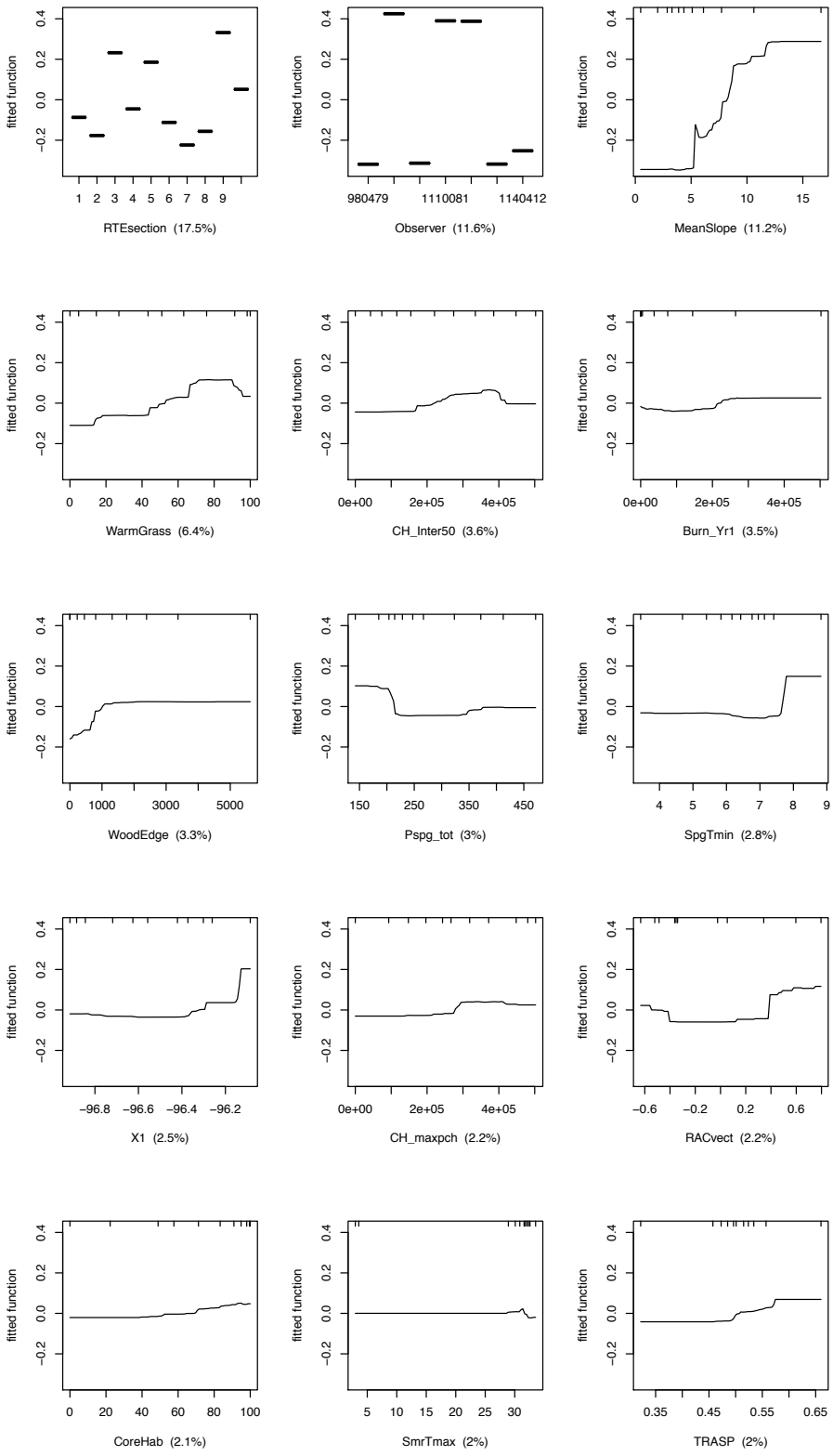
DICKCISSEL


fitted function
RTEsection (15.1%)
WoodEdge (11.6%)
Woodland (11.4%)
Pwin_tot (6.4%)
Observer (5.6%)
TRASP (5.5%)
Burn_Yr2 (5.5%)
Pspg_sd (5.3%)
SDslope (5.2%)
MeanSlope (5.1%)
Y2 (4.7%)
CH_Inter50 (4.7%)
WinTmin_mn (4.7%)
CoreHab (4.6%)
LULC_H (4.6%)

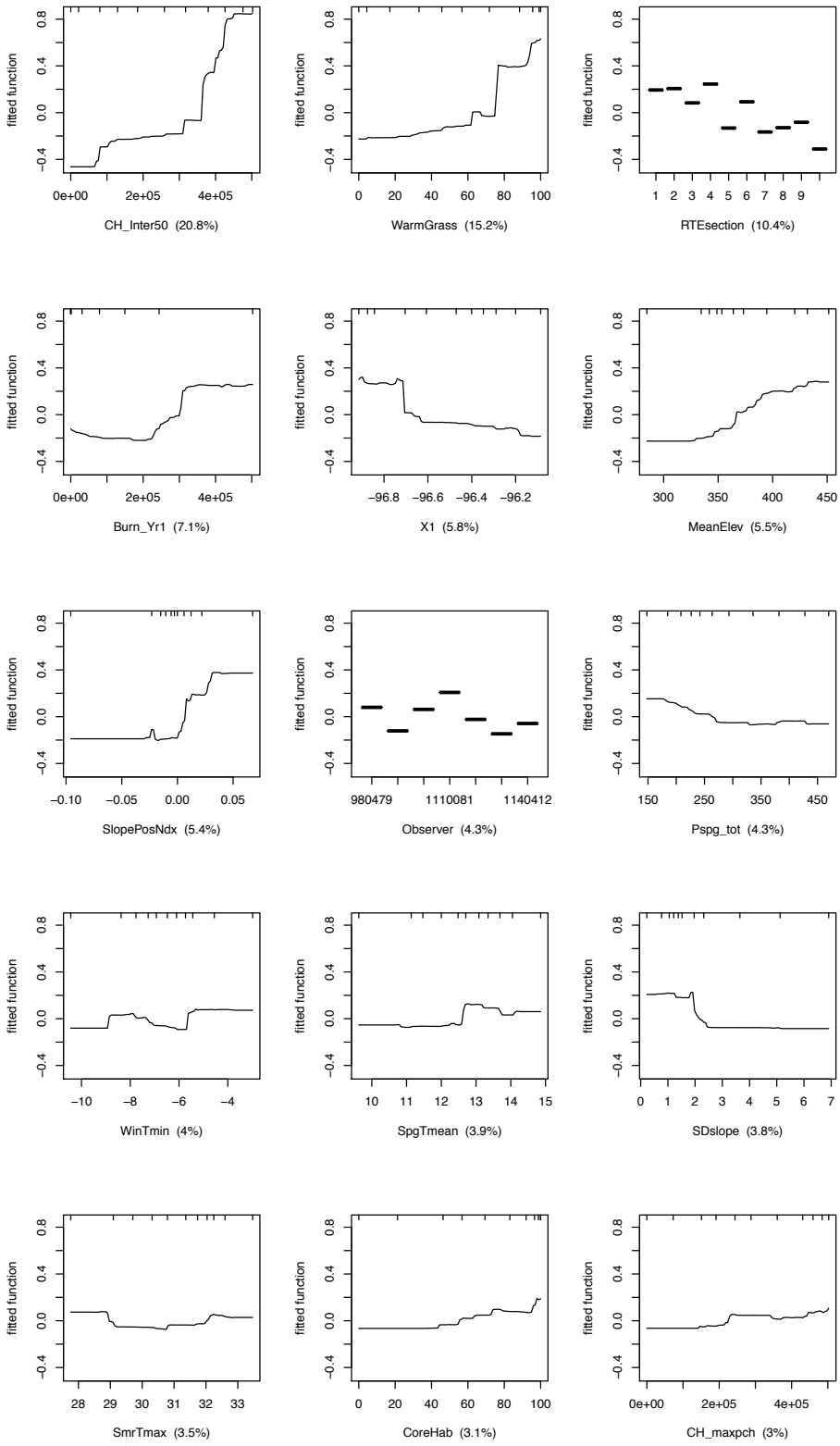
EASTERN MEADOWLARK



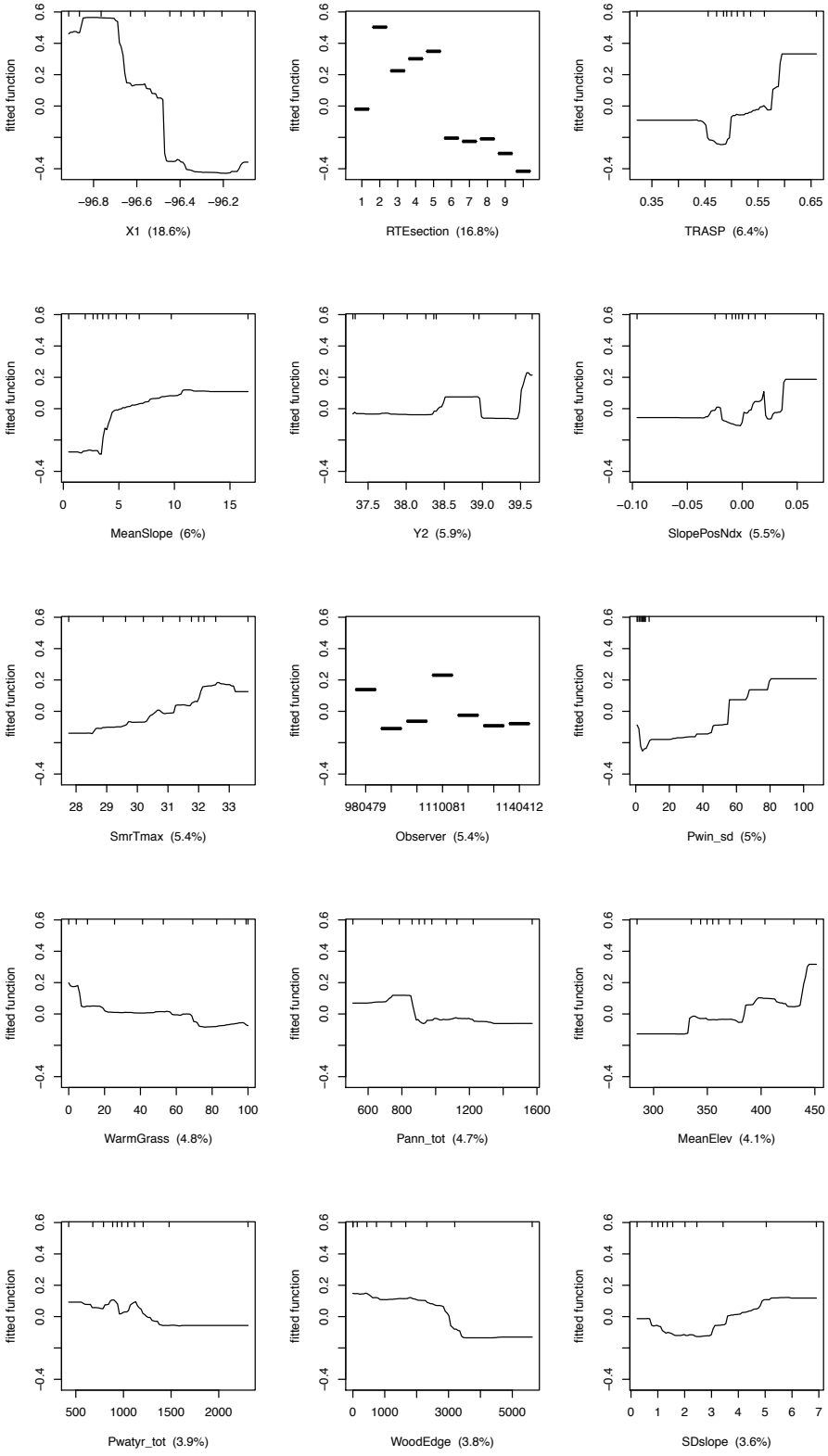
FIELD SPARROW



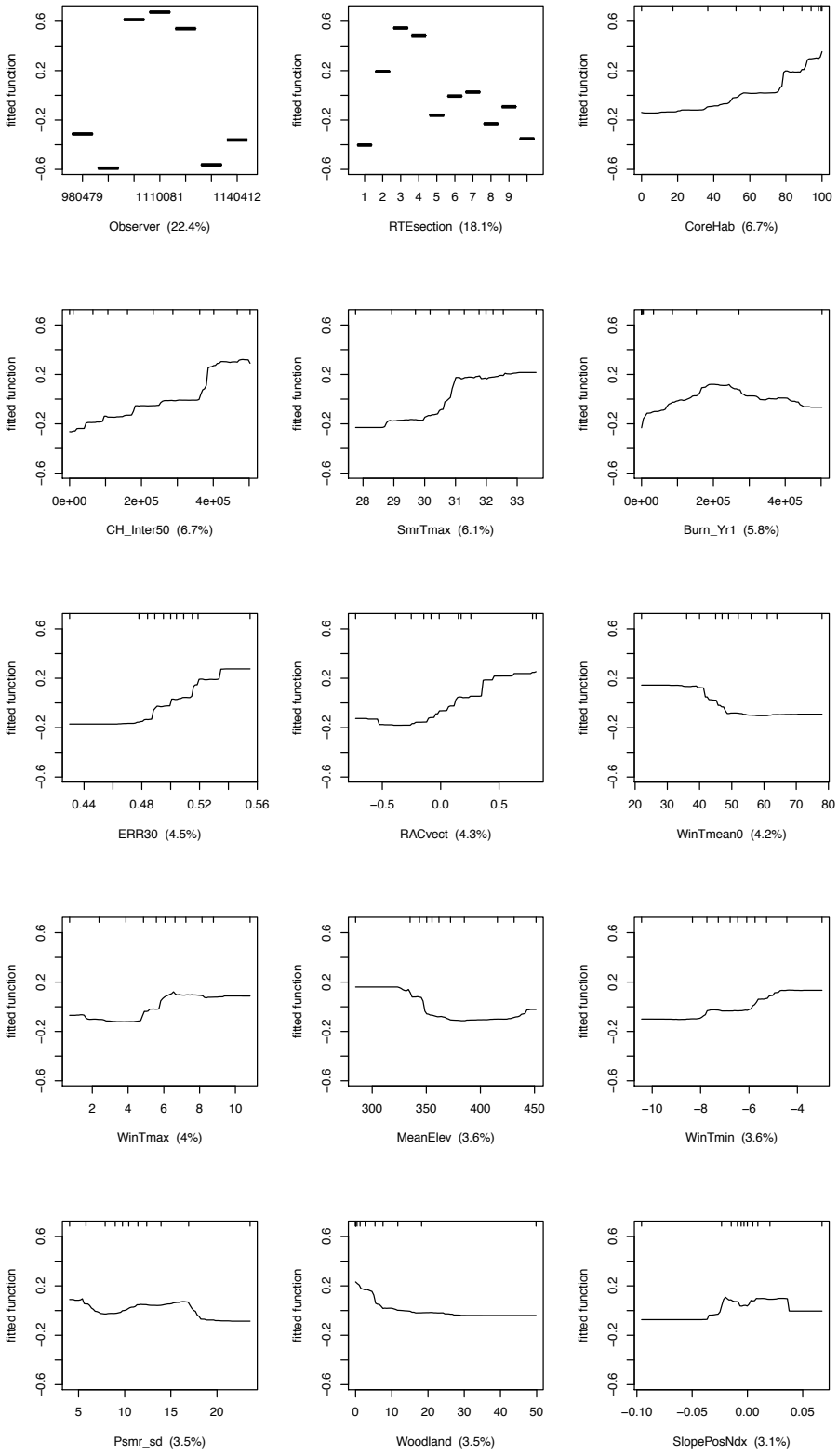
GRASSHOPPER SPARROW



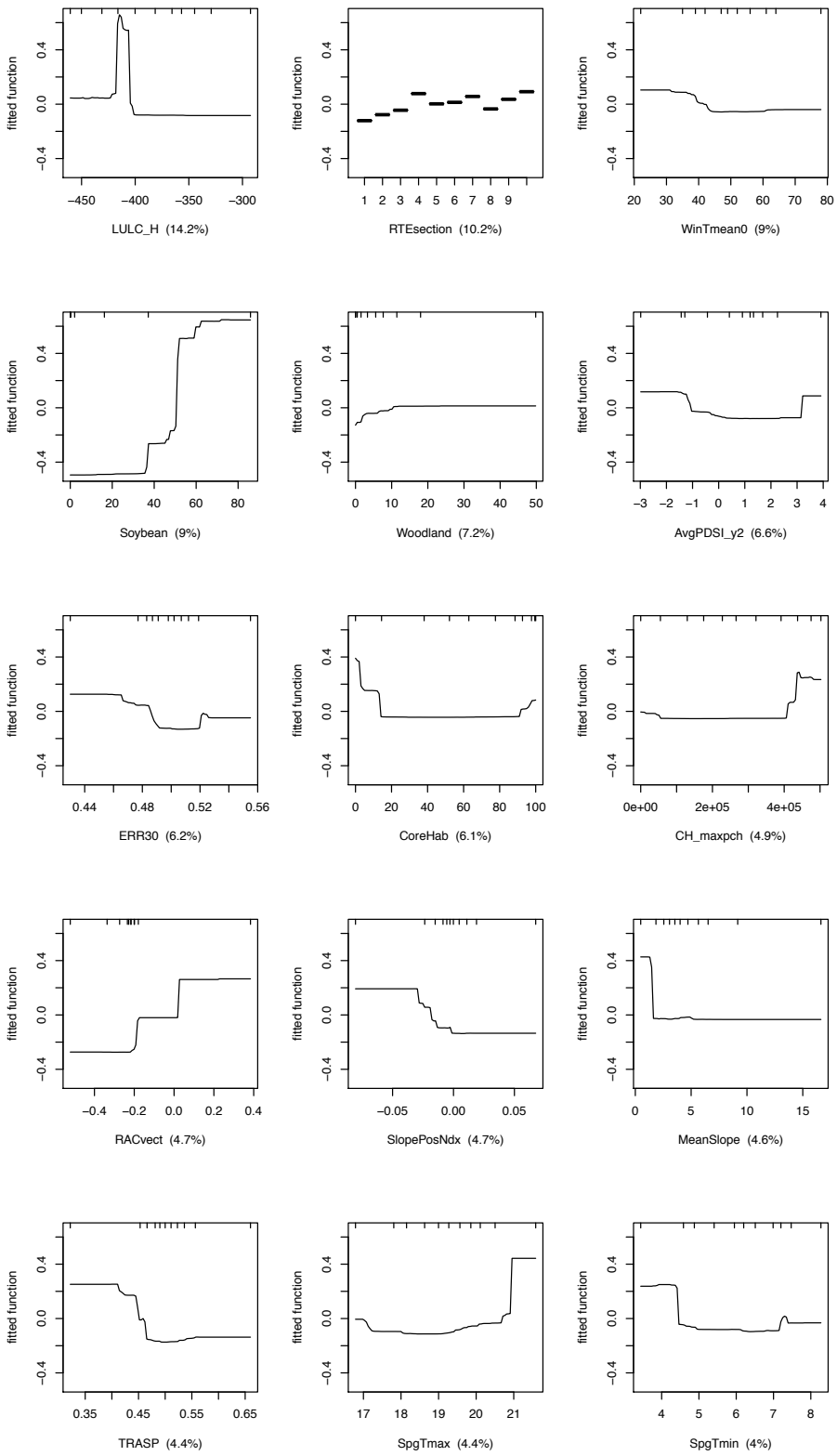
MOURNING DOVE



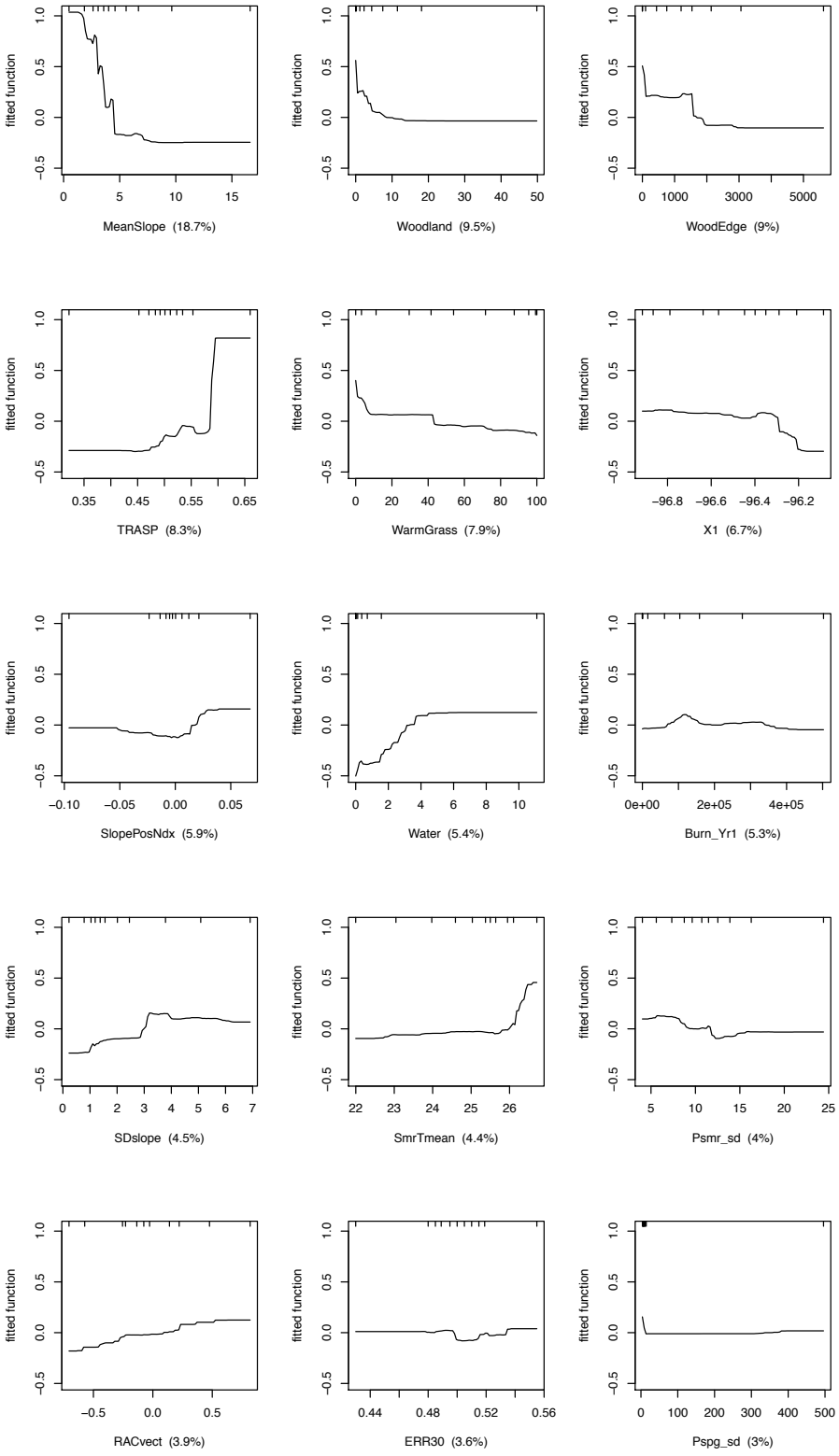
NORTHERN BOBWHITE



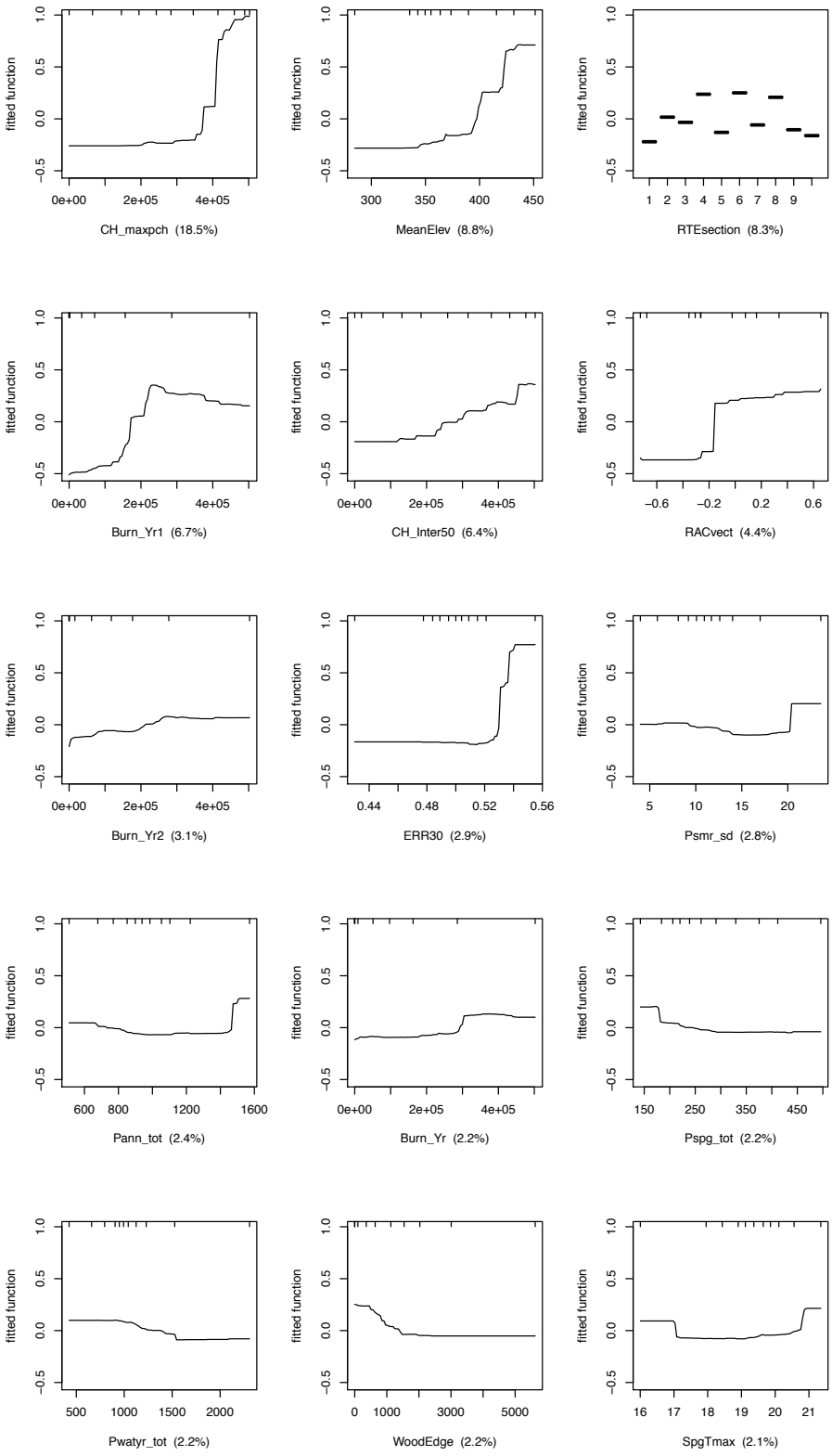
RED-HEADED WOODPECKER



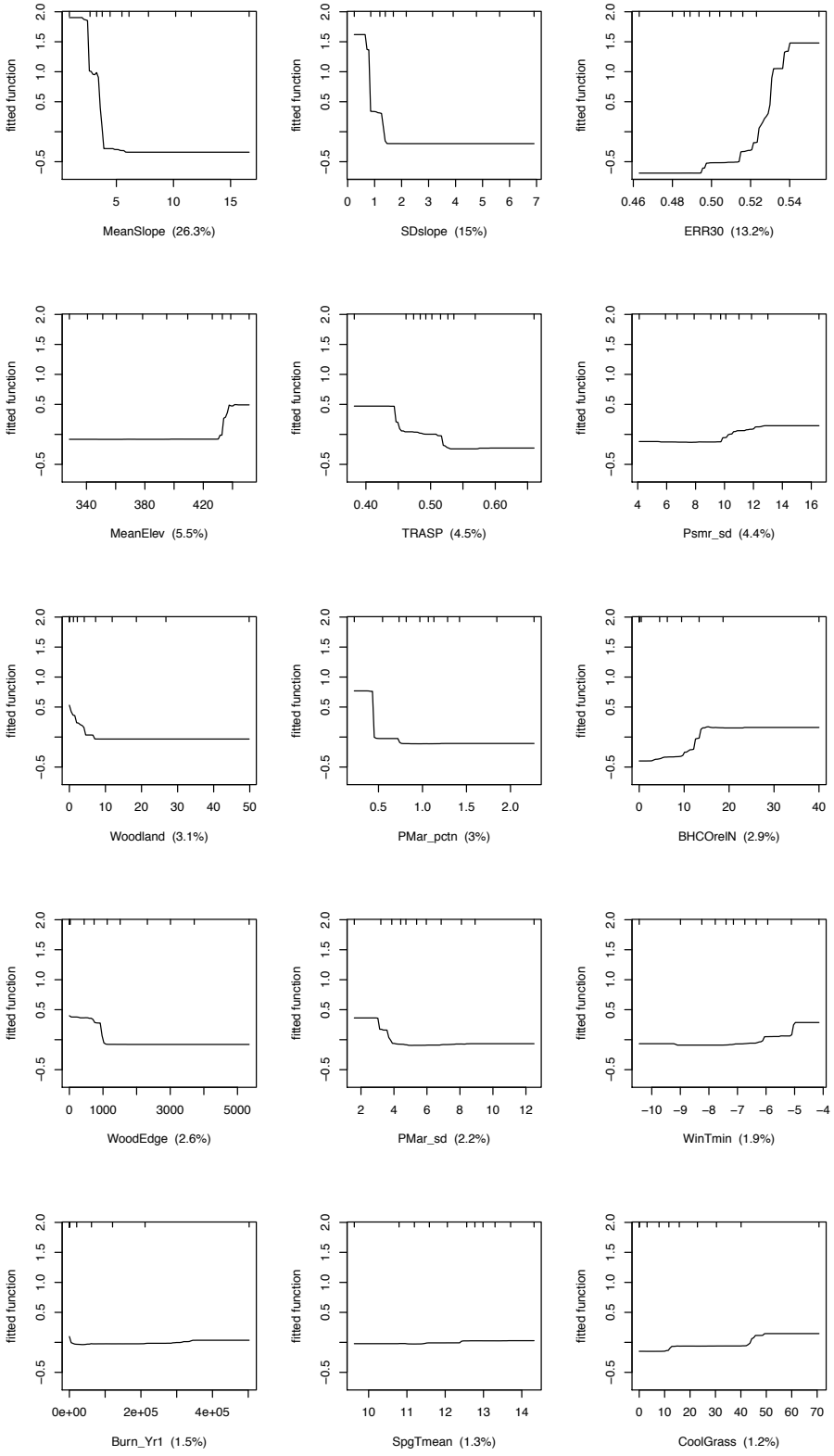
RED-WINGED BLACKBIRD



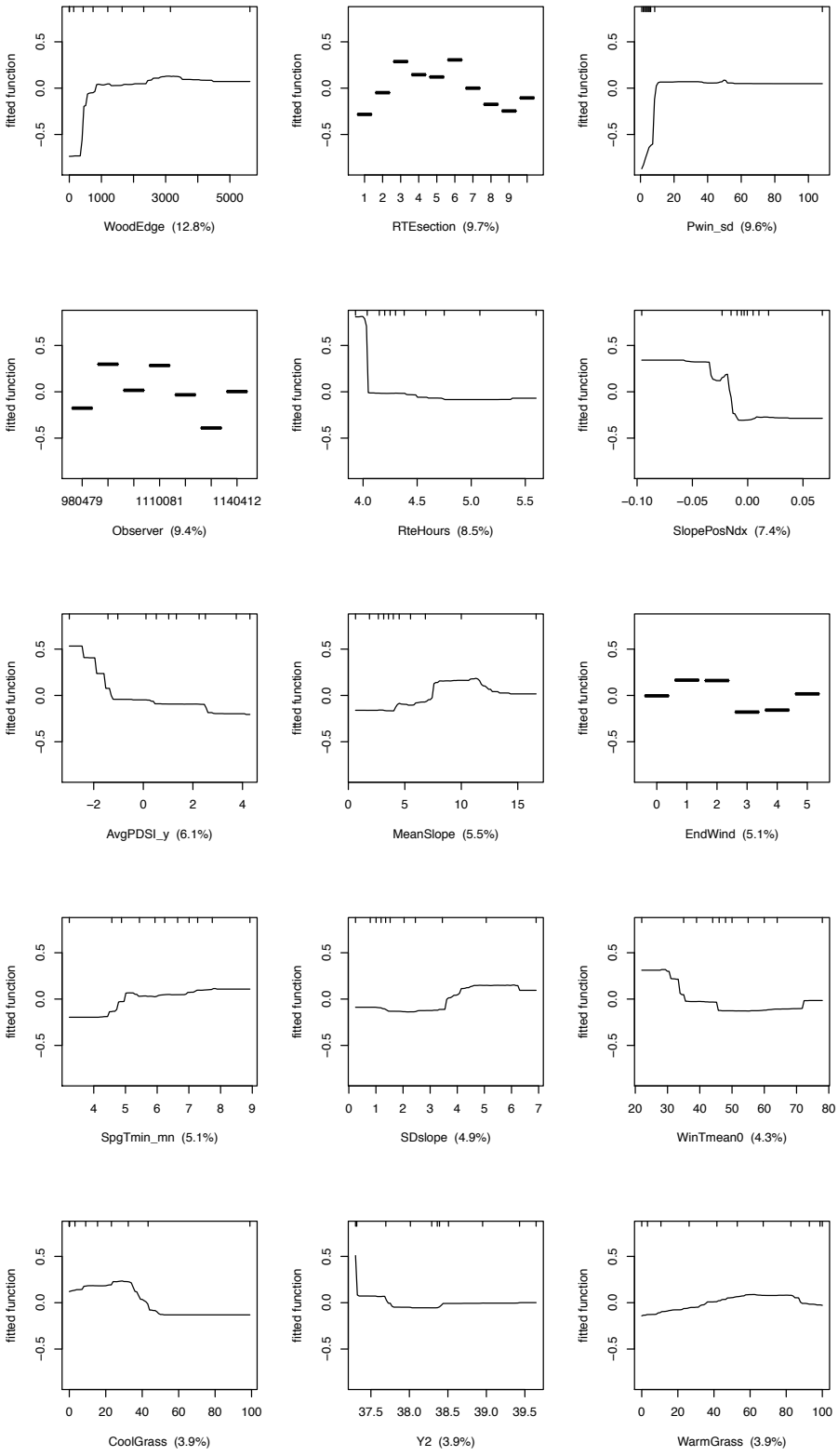
UPLAND SANDPIPER



WESTERN MEADOWLARK



YELLOW-BILLED CUCKOO



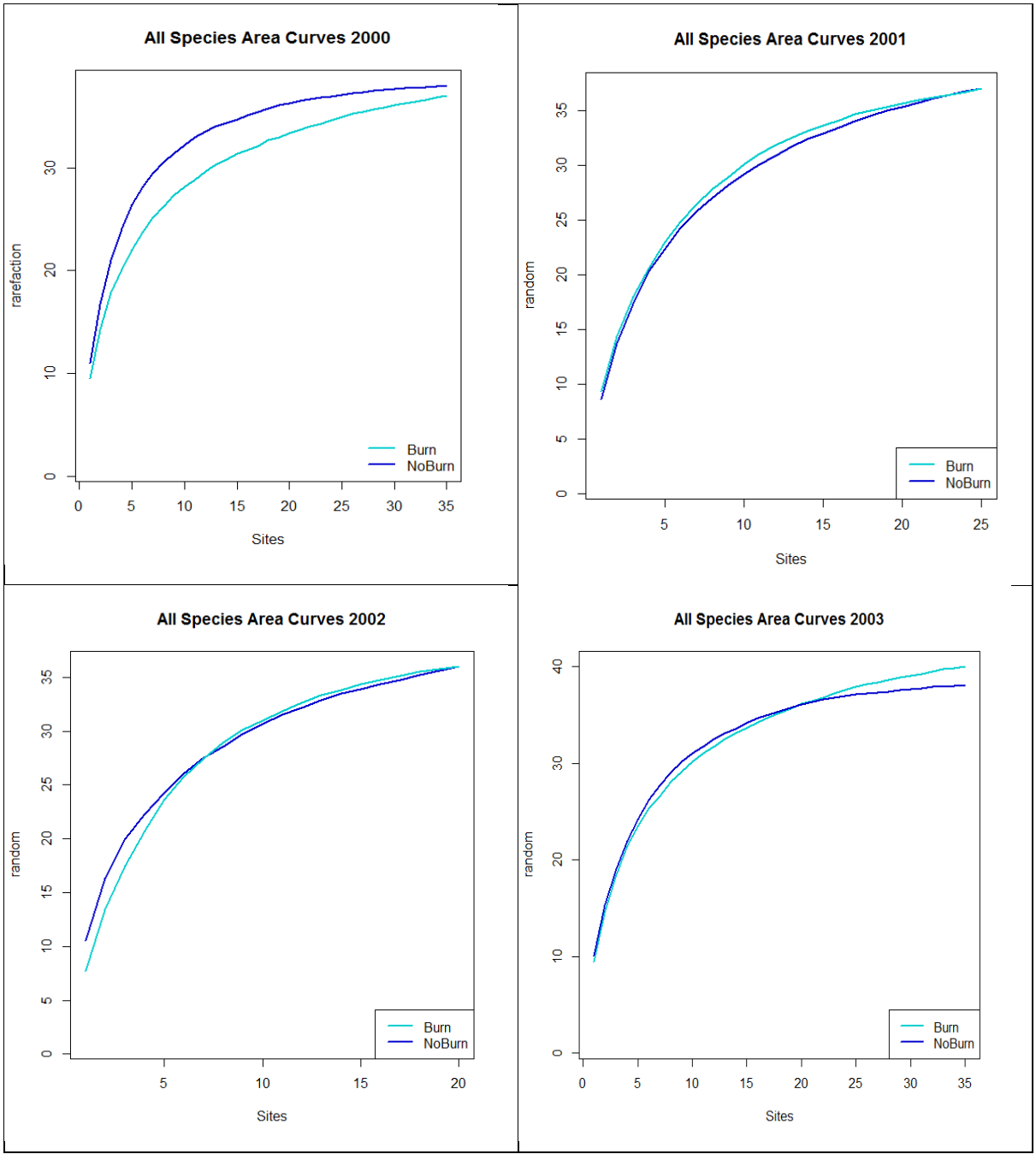
APPENDIX 6**:** Species list with relative and rank abundance in *Burn* and *NoBurn* sites.

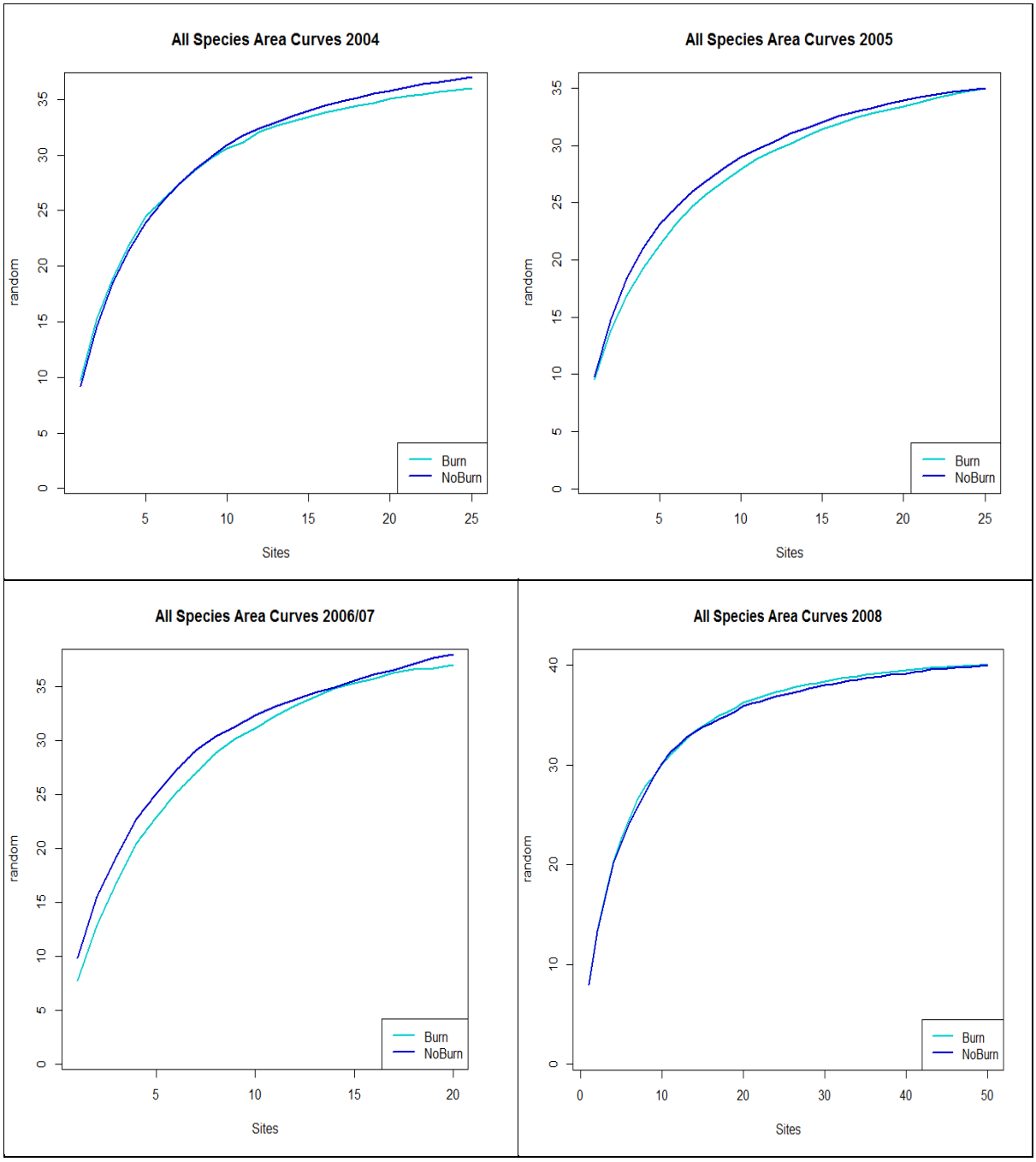
Common Name	Scientific Name	AOU Code	Rel N Total	Rank	Rel N Burn	Rel N NoBurn
American Crow	Corvus brachyrhynchos	AMCR	32.3	6	17.52	14.78
American Goldfinch	Spinus tristis	AMGO	6.65	25	3.8	2.85
American Robin	Turdus migratorius	AMRO	6.97	24	3.64	3.34
Baltimore Oriole	Icterus galbula	BAOR	6.63	26	3.36	3.26
Barn Swallow	Hirundo rustica	BARS	22.93	10	11.7	11.23
Bell's Vireo	Vireo bellii	BEVI	3.08	38	1.56	1.52
Blue Grosbeak	Passerina caerulea	BLGR	4.1	34	1.62	2.48
Blue Jay	Cyanocitta cristata	BLJA	5.87	29	2.77	3.09
Brown Thrasher	Toxostoma rufum	BRTH	7.79	22	3.84	3.95
Brown-headed Cowbird	**Molothrus ater**	**BHCO**	**45.1**	**3**	**23.83**	**21.27**
Carolina Wren	Thryothorus ludocicianus	CARW	3.57	37	1.45	2.12
Common Grackle	Quiscalus quiscula	COGR	11.05	17	4.54	6.52
Common Nighthawk	**Chordeiles minor**	**CONI**	**7.68**	**23**	**1.58**	**6.1**
Dickcissel	**Spiza americana**	**DICK**	**97.82**	**1**	**47.51**	**50.31**
Eastern Bluebird	**Sialia sialis**	**EABL**	**12.74**	**14**	**6.77**	**5.98**
Eastern Kingbird	**Tyrannus tyrannus**	**EAKI**	**8.22**	**20**	**2.97**	**5.25**
Eastern Meadowlark	**Sturnella magna**	**EAME**	**55.74**	**2**	**27.29**	**28.45**
Eastern Phoebe	Sayornis phoebe	EAPH	5.02	31	3.6	1.42
European Starling	Sturnus vulgaris	EUST	5.13	30	3.76	1.37
Field Sparrow	Spizella pusilla	FISP	9.13	19	4.34	4.78
Grasshopper Sparrow	**Ammodramus savannarum**	**GRSP**	**19.61**	**11**	**9.2**	**10.42**
Great Crested Flycatcher	Myiarchus crinitus	GCFL	10.5	18	7.18	3.32
House Sparrow	Passer domesticus	HOSP	3.87	35	2.39	1.48
Indigo Bunting	Passerina cyanea	INBU	13.45	13	9.15	4.3
Killdeer	**Charadruis vociferus**	**KILL**	**6.03**	**28**	**2.68**	**3.35**
Lark Sparrow	**Chondestes grammacus**	**LASP**	**4.4**	**32**	**1.57**	**2.83**
Mourning Dove	**Zenaida macroura**	**MODO**	**38.04**	**4**	**21.83**	**16.21**
Northern Bobwhite	**Colinus virginianus**	**NOBO**	**37.71**	**5**	**17.29**	**20.42**
Northern Cardinal	Cardinalis cardinalis	NOCA	23.06	9	12.02	11.05
Northern Mockingbird	Mimus polyglottos	NOMO	15.68	12	6.84	8.84
Orchard Oriole	Icterus spurius	OROR	3.06	39	1.18	1.88
Red-bellied Woodpecker	Melanerpes carolinus	RBWO	8.13	21	4.26	3.87
Red-winged Blackbird	**Agelaius phoeniceus**	**RWBL**	**26.19**	**7**	**14.55**	**11.64**
Scissor-tailed Flycatcher	**Tyrannus forficatus**	**STFL**	**6.11**	**27**	**3.01**	**3.09**
Tufted Titmouse	Baeolophus bicolor	TUTI	11.22	16	5.8	5.42
Upland Sandpiper	**Bartramia longicauda**	**UPSA**	**23.14**	**8**	**7.14**	**16**
Western Meadowlark	**Sturnella neglecta**	**WEME**	**3.81**	**36**	**3.27**	**0.54**
Wild Turkey	Meleagris gallopavo	WITU	4.4	33	2.11	2.29
Yellow-billed Cuckoo	Coccyzus americanus	YBCU	11.63	15	6.27	5.36

*Names in **bold** are facultative or obligate grassland species*

*****American Ornithological Union 4-letter code (Pyle & DeSante, 2014)*

APPENDIX 7: Sample-based rarefaction curves for the *all species* group, showing differences in species richness between *Burn* (cyan curve) and *NoBurn* (blue curve).




All Species Area Curves 2004
random
Sites
Burn
NoBurn
All Species Area Curves 2005
random
Sites
Burn
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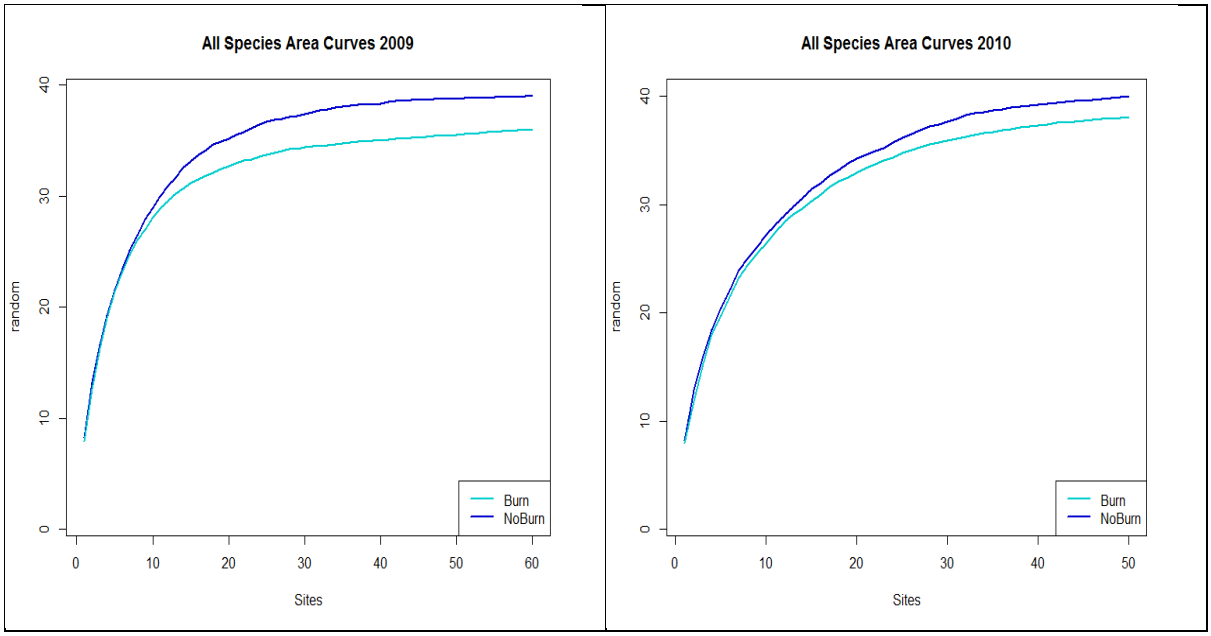
All Species Area Curves 2006/07
random
Sites
Burn
NoBurn
All Species Area Curves 2008
random
Sites
Burn
NoBurn


All Species Area Curves 2009
random
Sites
Burn
NoBurn
0
10
20
30
40
50
60
All Species Area Curves 2010
random
Sites
Burn
NoBurn
0
10
20
30
40
50

APPENDIX 8: Diversity statistics for *all species*, *grassland*, and *shrub-woodland* species groups. Each calculated diversity ratio was calculated as the mean diversity for *Burn sites* divided by the mean diversity value for *NoBurn* sites. The magnitude of difference between mean diversity values (1-diversity ratio) follows each diversity ratio. Positive values indicate that Burn sites had lower diversity for a particular statistic (Burn<S). Negative values indicate the NoBurn sites (NoBurn<S) had lower diversity for that statistic. S=species richness, H'=Shannon entropy, D=Simpson's concentration, and E=Evenness. All diversity indices calculated in effective number of species format.

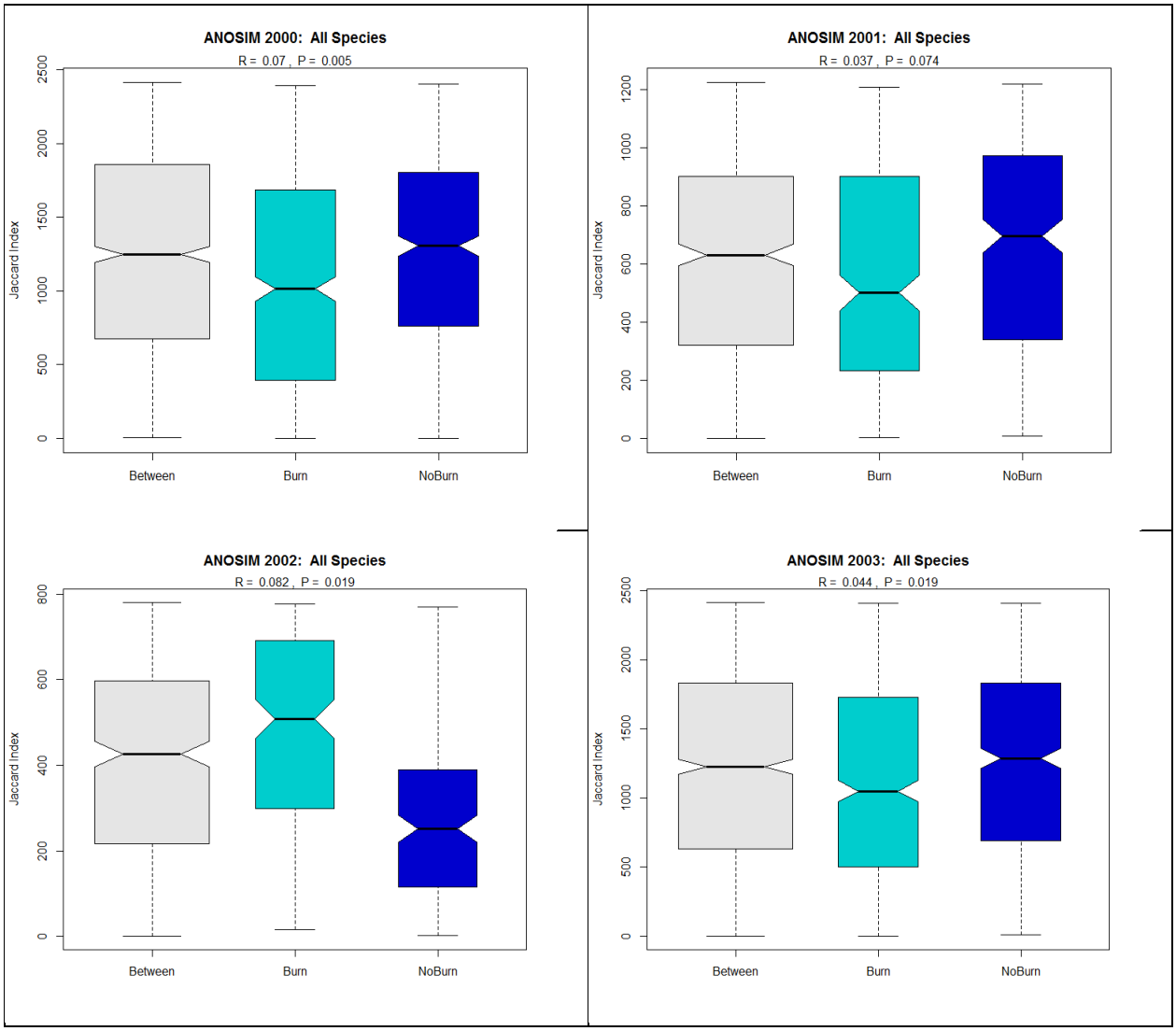
Model Year	Group	RICHNESS	Burn<S	NoBurn<S	SHANNON	Burn<H'	NoBurn<H'
2000	all species	0.824	17.60		0.853	14.66	
	grassland	1.047			1.053		-5.26
	shrub-wood	0.634	36.62		0.674	32.65	
2001	all species	1.053		-5.31	1.067		-6.71
	grassland	1.219		-21.90	1.194		-19.39
	shrub-wood	0.842	15.79		0.905	9.51	
2002	all species	0.762	23.81		0.744	25.57	
	grassland	0.773	22.69		0.756	24.42	
	shrub-wood	0.793	20.72		0.775	22.50	
2003	all species	0.940	6.00		0.959		
	grassland	1.095		-9.52	1.112		-11.22
	shrub-wood	0.801	19.90		0.822	17.82	
2004	all species	0.983			1.002		
	grassland	1.049			1.061		-6.06
	shrub-wood	0.909	9.09		0.889	11.10	
2005	all species	1.000			0.995		
	grassland	1.013			1.032		
	shrub-wood	0.980			0.950	5.01	
2006/07	all species	0.765	23.53		0.853	14.72	
	grassland	0.893	10.67		0.949	5.08	
	shrub-wood	0.654	34.62		0.699	30.14	
2008	all species	1.010			1.025		
	grassland	1.057		-5.71	1.078		-7.80
	shrub-wood	0.954			0.955		
2009	all species	0.986			1.020		
	grassland	1.105		-10.53	1.159		-15.94
	shrub-wood	0.862	13.75		0.873	12.73	
2010	all species	0.983			0.985		
	grassland	1.059		-5.86	1.067		-6.72
	shrub-wood	0.883	11.68		0.875	12.47	

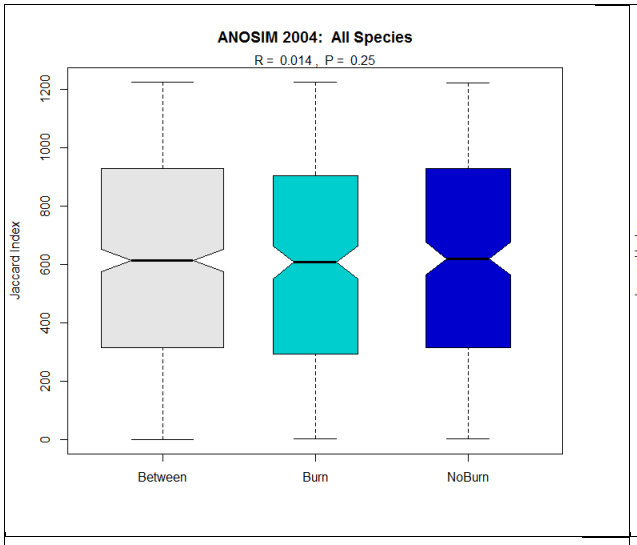
All diversity ratios calculated as Burn/NoBurn

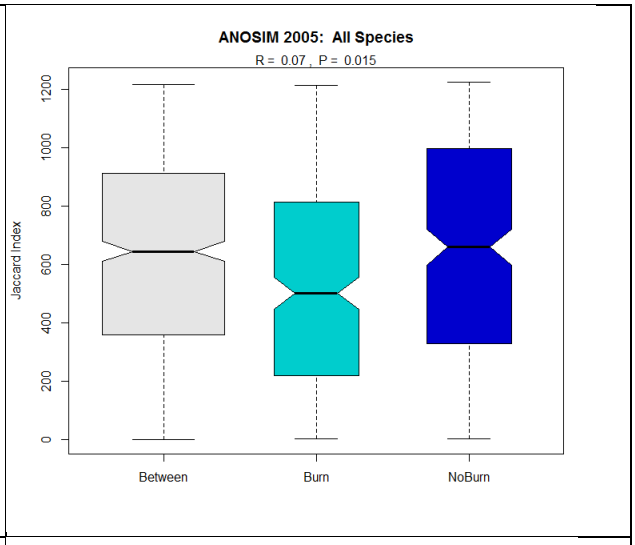
Model Year2	Group2	SIMPSON	Burn<D	NoBurn<D	EVENNESS	Burn<E	NoBurn<E
2000	all species	0.880	12.02		1.026		
	grassland	1.050			1.013		
	shrub-wood	0.710	28.97		1.040		
2001	all species	1.065		-6.52	0.998		
	grassland	1.174		-17.45	0.966		
	shrub-wood	0.937	6.33		1.055		-5.534
2002	all species	0.724	27.58		0.992		
	grassland	0.736	26.43		1.012		
	shrub-wood	0.761	23.92		0.976		
2003	all species	0.968			1.017		
	grassland	1.109		-10.91	1.005		
	shrub-wood	0.842	15.76		1.025		
2004	all species	1.015			1.023		
	grassland	1.057		-5.66	1.007		
	shrub-wood	0.881	11.87		0.995		
2005	all species	0.983			0.990		
	grassland	1.035			1.004		
	shrub-wood	0.939	6.12		0.981		
2006/07	all species	0.931	6.93		1.114		-11.41
	grassland	0.962			1.082		-8.16
	shrub-wood	0.724	27.65		1.066		-6.59
2008	all species	1.046			1.004		
	grassland	1.092		-9.19	1.009		
	shrub-wood	0.963			1.012		
2009	all species	1.047			1.032		
	grassland	1.186		-18.63	1.037		
	shrub-wood	0.883	11.73		1.010		
2010	all species	0.985			1.009		
	grassland	1.072		-7.24	1.012		
	shrub-wood	0.864	13.59		1.003		

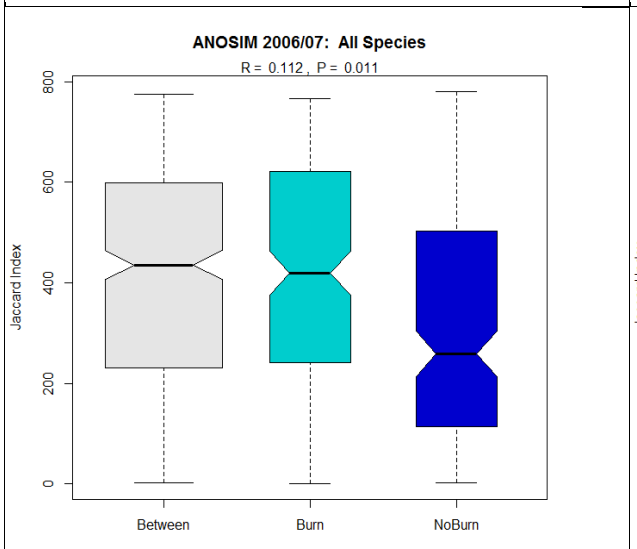
All diversity ratios calculated as Burn/NoBurn

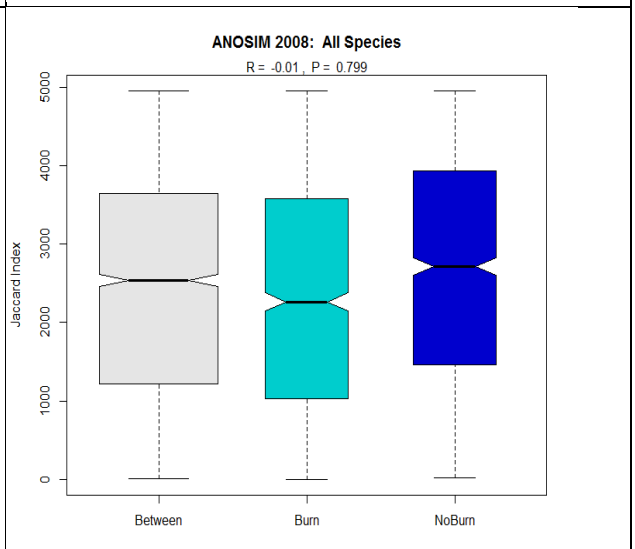
APPENDIX 9: Analysis of Similarity for the *all species* group comparing within and between group differences in community similarity based on burn status.

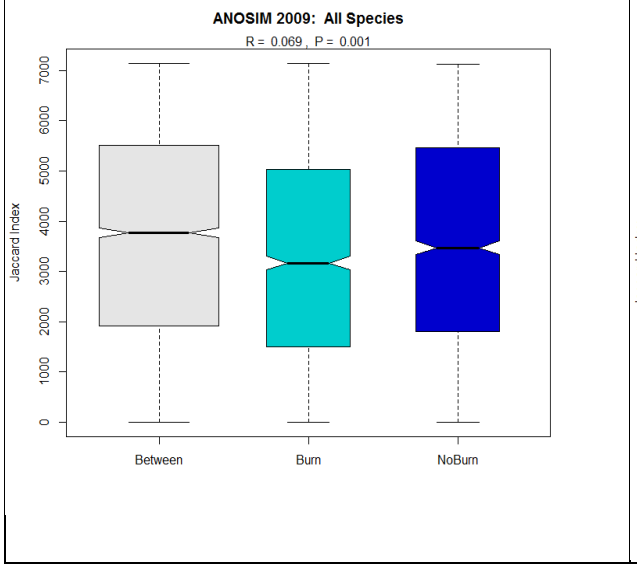


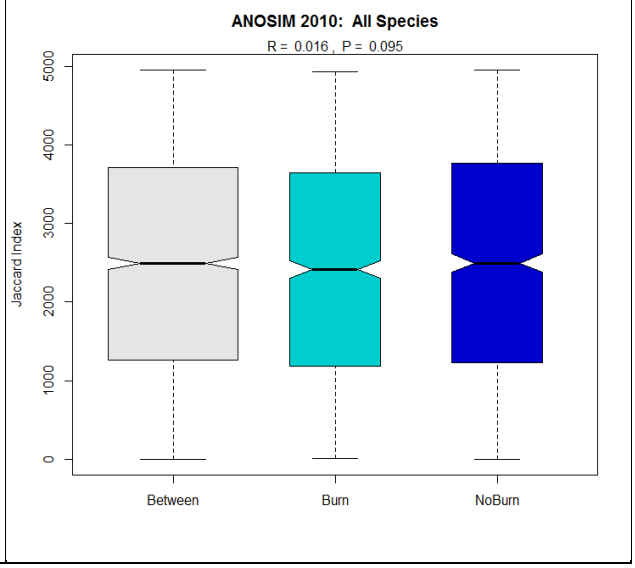

ANOSIM 2004: All Species
R = 0.014 , P = 0.25
Jaccard Index
0
200
400
600
800
1000
1200
Between
Burn
NoBurn


ANOSIM 2005: All Species
R = 0.07 , P = 0.015
Jaccard Index
0
200
400
600
800
1000
1200
Between
Burn
NoBurn


ANOSIM 2006/07: All Species
R = 0.112 , P = 0.011
Jaccard Index
0
200
400
600
800
Between
Burn
NoBurn


ANOSIM 2008: All Species
R = -0.01 , P = 0.799
Jaccard Index
0
1000
2000
3000
4000
5000
Between
Burn
NoBurn

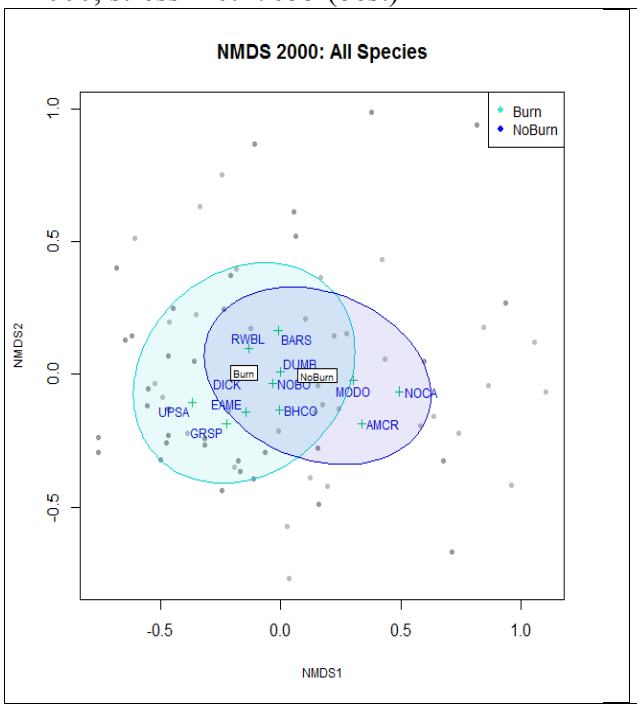

ANOSIM 2009: All Species
R = 0.069 , P = 0.001
Jaccard Index
0
1000
2000
3000
4000
5000
6000
7000
Between
Burn
NoBurn


ANOSIM 2010: All Species
R = 0.016 , P = 0.095
Jaccard Index
0
1000
2000
3000
4000
5000
Between
Burn
NoBurn

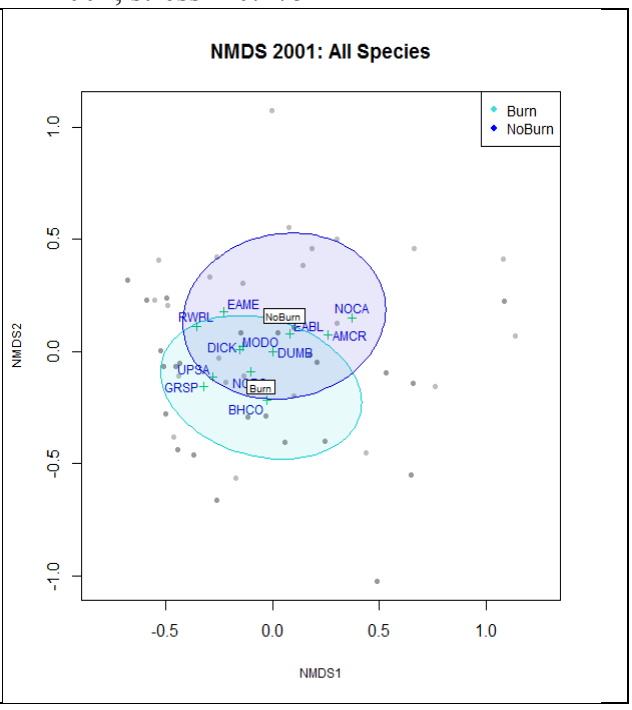
APPENDIX 10: Non-metric multidimensional scaling (NMDS) ordination plots based on distance matrices of the binary Jaccard Index of community similarity between *Burn* and *NoBurn* sites paired with Euclidean distance between those sites. Sites plotted closer together in ordination space have more similar avian communities. Stress values measure the disagreement in the rank order of Jaccard Index values in the original data and that in ordination space; lower numbers indicate better agreement. Stress values above 0.2, mean that the ordination results must be interpreted with caution; values between 0.1 and 0.2 are fair (McGarigal, et al., 2000).

Plots are shown for the *all species* group. Stress values are listed above each corresponding plot. Ellipses (standard deviation) of each are drawn around *Burn* (cyan) and *NoBurn* (blue) group centroids. Small gray circles represent site locations; slightly darker gray circles are *Burn* stops. Green crosses represent the top 30% most abundant species, labeled using AOU Codes (see Chapter 3, Table 2); "DUMB" identifies the dummy species added to each data set.

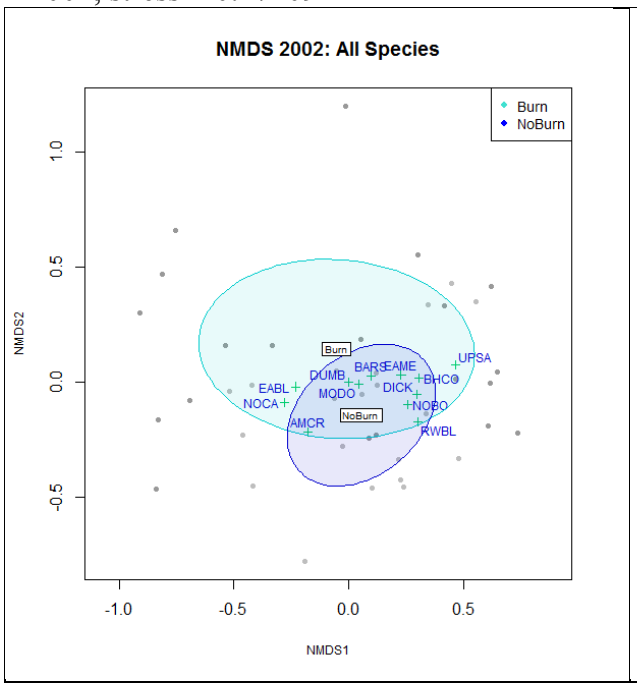
2000, stress = 0.17055 (best)



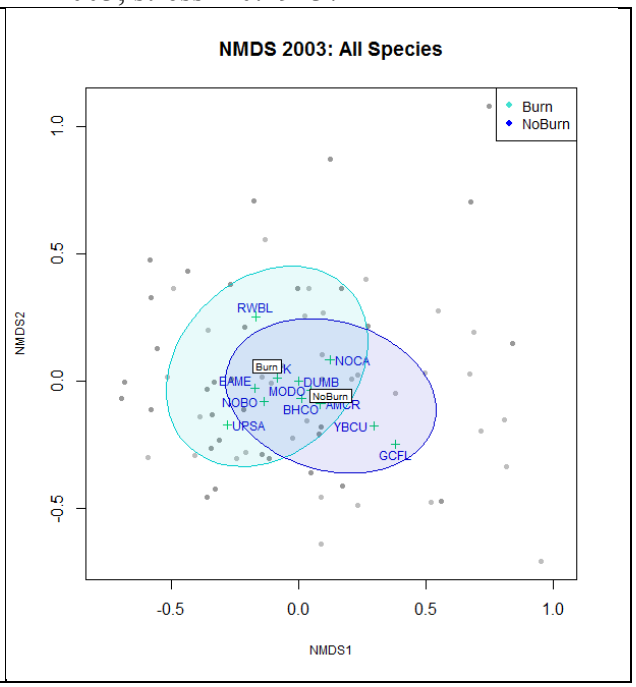
2001, stress = 0.17512



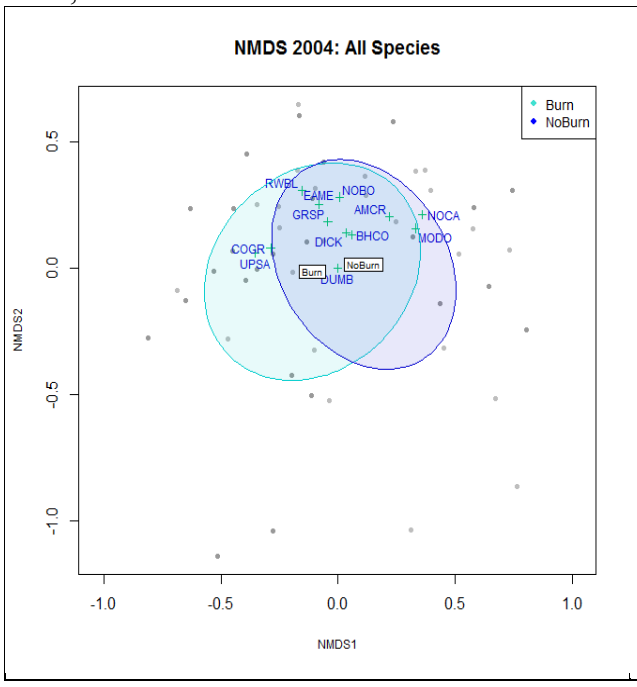
2002, stress = 0.17409



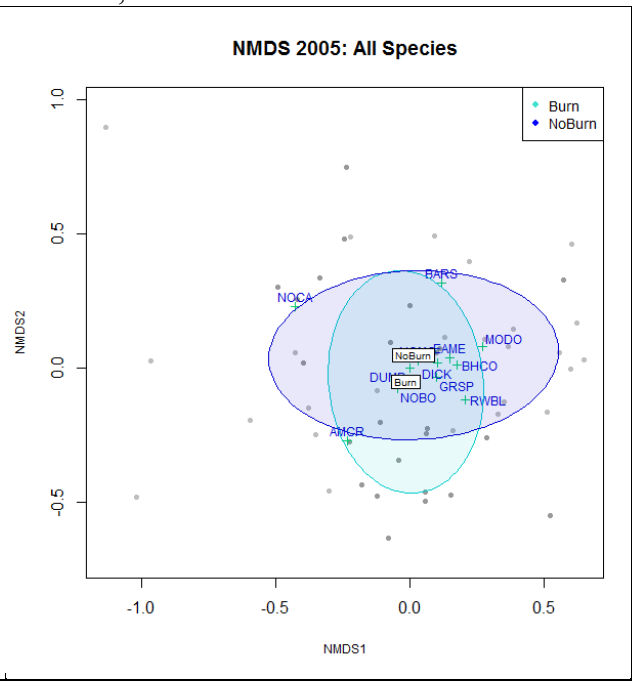
2003, stress = 0.19237



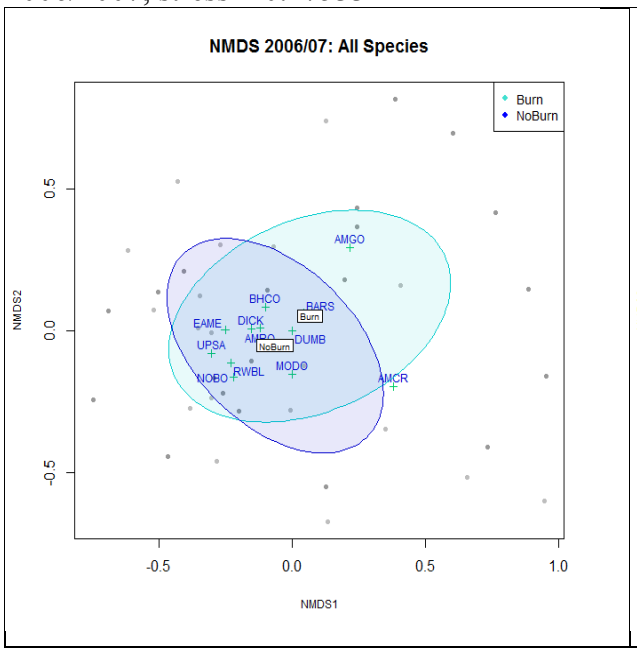
2004, stress = 0.17348



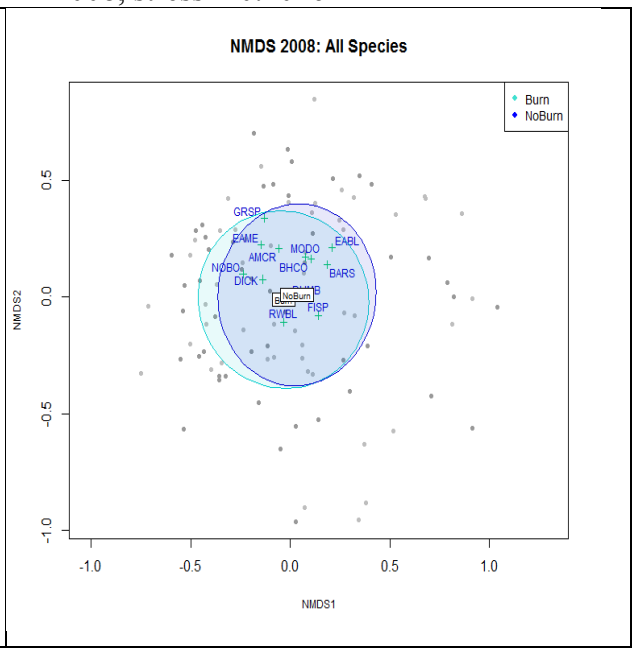
2005, stress = 0.18002



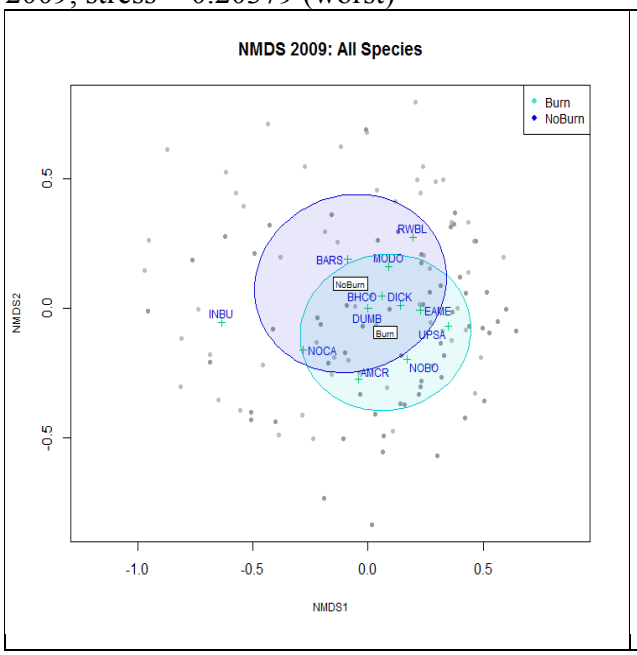
2006/2007, stress = 0.17533



2008, stress = 0.20162



2009, stress = 0.20379 (worst)



2010, stress = 0.19429